

## ERICALES

The newly circumscribed and arranged Ericales are one of the success stories of the New Phylogeny whereby some 25 families, 346 genera, 11,515 species, formerly scattered with variation among three classes (Asteridae, Dilleniidae, and Rosidae) are now assembled in a strongly supported monophyly that is sister to the asterids. The exact arrangements of the constituent families vary among the five main recent studies<sup>1-5</sup>, and significant analytic problems remain to be resolved. In particular, there are problems in balancing the advantages of greater taxon sampling with increased missing data, and with conflicts between Bayesian approaches and those of Maximum Parsimony. Also, an important study of the Sapotoideae subfamily of the Sapotaceae found that rate changes might vary not only among genetic markers but also over time. STEVENS *loc. cit.* discusses most of the variant arrangements and possible sister relationships.

A technical description of the Ericales would require a great many exceptions and explanations due to the heterogeneity in the order and the lack of strong morphological synapomorphies. What can be said broadly is that some Ericales bear haplostemonous flowers (one series of stamens, one opposite each petal), while some bear ovules with a single integument, but no member of the Ericales shows both conditions in combination, which distinguishes them from the typical condition of the asterids proper. Furthermore, the current interpretation is that the fused corolla that characterizes several of the families arose independently, while the diplostemonous condition (two whorls of stamens, one opposite the calyx lobes, one opposite the petals) likely arose from an ancestral haplostemonous condition.

A generalized description of a typical member of the Ericales would be a woody plant with relatively long unbranched twigs that bear a terminal cluster of spirally arranged leaves. Some families accumulate aluminum and the leaves dry shades of yellow-green, red and black. The leaf stalk is without swellings and joins the stem with a clean node or only with a hint of paired glands, while the twig apex is an unprotected slender, pointed, and somewhat sinuous tip covered with silky hairs. The blade is elliptic, weakly toothed with laminar glands of some sort. The flower bears a single superior ovary and sharply pointed style; the calyx is strong and persistent, the petals sometimes showy, more or less fused near the base or

fully cup-like; the stamens twice or more the number of petals.

Most Ericalean families diverge from that general description in one or more significant ways. Symplocaceae bear inferior ovaries. The Sapotaceae are odd in that many species have strong stipules and copious white exudate, features not found in other Ericalean families. Ebenaceae are characterized by an upright stem with clusters of short internodes from which the lateral branches are arrayed like spokes of a wagon-wheel.

The families of the Ericales in Asia divide somewhat imperfectly between the more basal families that are shade-loving plants, species-rich and abundant in the lowland equatorial forests (Barringtoniaceae, Sapotaceae and Ebenaceae) and sun-loving plants especially prevalent at elevations around 1000 m (Pentaptylloaceae, Theaceae, Symplocaceae, Ericaceae, Clethraceae, Actinidiaceae). The latter families are also found in lower elevations as uncommon forest trees over sandstones, white sands, *kerangas* vegetation, exposed hilltops, and other nutrient poor habitats (e.g., *Adinandra dumosa*, *Staphyllea*, the occasional *Rhododendron*, or other Ericaceae as mangrove epiphytes).

The suggested division between upland and lowland taxa of the Ericales, if further understood in the context of phylogeny and geography, will someday tell a story that will significantly change our thinking about the rise and spread of flowering plants. As an indication of the complexities involved, we might envision ourselves transported to South America to explore the tropical Ericales there. (See, for example, the relevant family descriptions in GENTRY *loc. cit.* and *Flora Neotropica*.) In the lowlands we would be more than a little bewildered. The Lecythidaceae look much like *Barringtonia* in leaf and twig but the flowers and fruit are all wrong and vary wildly. We will find plenty of *nyatoh*, recognizable enough as the family Sapotaceae, but in the American tropics we once again find a far richer heterogeneity of floral detail and far greater abundance. By contrast, the ebonies, of which we would expect a dozen abundant species in a lowland forest in Asia, are of far lesser abundance and richness. We might latch on to a lowland *Ardisia* as a point of common reference; it certainly looks the same in Asia and America, and yet with more exploration and a change to higher elevations and we find a dozen other Myrsinaceae genera in America very different from anything in Asia. But if we persist and continue to climb to 1500 m or so, we soon find ourselves in more familiar Ericalean territory, for not just the families but the genera themselves become familiar: *Saurauia*, *Clethra*, *Styrax*, *Symplocos*, *Ternstroemia* and a host of shrubs in the Ericaceae. In flower, fruit and leaf, all look and behave much the same as their Asian congeners.

By what fortunes of history did this arrangement come about? No one yet knows, but the first step in a solution lies in the strong phylogeny that is now emerging.

<sup>1</sup>Källersjö, M. *et al.* 2000. American Journal of Botany. 87:1325-1341.

<sup>2</sup>Anderberg, A. *et al.* 2002. American Journal of Botany. 89: 677-687.

<sup>3</sup>Bremer, B. *et al.* 2002. Molecular Phylogenetics and Evolution. 24: 274-301.

<sup>4</sup>Geuten, K. *et al.* 2004. Molecular Phylogenetics and Evolution. 31: 711-729.

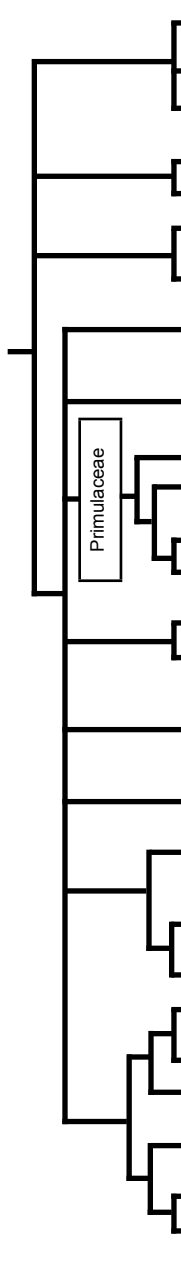
<sup>5</sup>Schönenberger, J. *et al.* 2005. International Journal of Plant Sciences, 166: 265-288.

<sup>6</sup>Smedmark, J. *et al.* 2006. Molecular Phylogenetics and Evolution. 39: 706-721.

<sup>7</sup>Jansen, S. *et al.* 2004. Plant Biology (Stuttgart) 6: 498-505.

Phylogeny of Ericales

The phylogeny drawn here is based on the recent molecular studies cited in the family introduction<sup>1-5</sup>. Families and diversity estimates follow STEVENS *loc. cit.* with only minor modifications such as the segregation of the Barringtoniaceae. See the cited papers and STEVENS *loc. cit.* for alternative clusterings. Those families that strongly accumulate aluminum (following Jansen *et al.*<sup>7</sup>) are indicated with a yellow box. APG III suggests an expanded Primulaceae for the strong clade of four families in that group.

Family		Diversity and Distribution	Trees of Tropical Asia	
	Balsaminaceae	2/1000, fleshy herbs, N Temperate, Paletropical mountains.	0	Lowland Ericales rich and abundant in lowland equatorial forests, non-aluminum accumulating, rich soils, wet and dry ground
	Marcgraviaceae	7/130, lianas, Neotropical.	0	
	Tetrameristaceae	3/5, trees, American mangrove, Asian swamp forests.	1/1, <i>Tetramerista glabra</i> , swamp forest.	
	Polemoniaceae	18/385, herbs, not Paletropical.	0	
	Fouquieriaceae	1/11, shrubs, SW N America.	0	
	Barringtoniaceae	6/58, Paletropical.	5/50, especially lowland wet forest, riversides, some dry seasonal, fire-prone.	
	Lecythidaceae	19/240, African and American tropics.	0	Upland Ericales rich and abundant ver 1000 m, in equatorial lowlands on sand, full sun, streams, some aluminum accumulating.
	Sapotaceae	53/1100, global tropical.	13/250, widespread, mainly lowlands, many rare species, mostly low abundance.	
	Ebenaceae	5/458, mostly Paletropical.	1/180, especially lowland equatorial, but some species in all of tropical Asia.	
	Maesaceae	1/150, Paletropical northward.	1/25, especially along streams.	
	Theophrastaceae	6-9/ 105, Neotropical and warm temperate.	0	
	Primulaceae	9/900, mostly N Hemisphere.	0	
	Myrsinaceae	41/1435, pantropical and N Hemisphere.	5/200, widespread, lowland and mountains, some abundant.	
	Sladeniaceae	2/3, small trees, Africa, S China.	0	
	Pentaphylaceae	12/337, tropical, subtropical.	6/70, especially <i>Adinandra</i> and <i>Ternstroemia</i> , exposed uplands and lowlands over nutrient poor soils.	
	Theaceae	7/200, small trees, tropics and subtropics, especially Asia.	5/50-70, whether <i>Schima</i> is 1 or 20, mountains, also lowlands over poor soils.	
	Mitrastemonaceae	1/2, root parasites, scattered tropical	0	
	Symplocaceae	2/320, tropical, not Africa.	2/80, especially <i>Symplocos</i> , full sun in mountains, lowand gaps and roadsides on poor soils.	
	Styracaceae	11/160, tropical, subtropical, not Africa,	5/20, some montane, especially strongly sry seasonal.	
	Diapensiaceae	6/18, herbs, high latitudes.	0	
	Actinidiaceae	3/355, E Asia, tropics and American tropical mountains.	1/30, mountains and lowlands, especially near water, wet forest gaps.	
	Roridulaceae	1/2, S Africa, shrubs.	0	
	Sarracenaceae	3/15, pitcher plants, America N and S.	0	
	Clethraceae	2/75, woody, tropical montane, America and Asia.	1/6, sull sun, montane.	
	Cyrillaceae	2/2, E Americas.	0	
	Ericaceae	126/4000, global, poor in tropical lowlands.	9/150, montane full sun, lowlands on white sand, poor soils, mangrove.	

## OTHER ASTERIDS: ERICALES

## TETRAMERISTACEAE

NAME: From the genus *Tetramerista*, as below.

OVERVIEW: This small family combines three monotypic genera. *Tetramerista glabra* is a well-known swamp forest tree of our region. *Pentamerista neotropica* proved to be an astonishingly similar looking tree first described only in 1952 from the Guayana Highlands of northern S America. To these two we add the American mangrove, *Pelliciera rhizophorae*. All three species share a similar sort of vegetative appearance, a pair of bracteoles beneath each flower, a long style, and the leaves dry dark brown-purple.

**TETRAMERISTA.** [Greek, in reference to the flowers with parts in fours.] Monotypic, *Tetramerista glabra*, from Sumatra, Malaya and Borneo, generally well-known as *punah* in Malay, *kepoyang* in Iban (not *kepayang*) and generally as *tuyut* in Sabah. The genus is still repeatedly cited in floras and encyclopedias as including three species. The four basionyms are disposed as follows: *Tetramerista glabra* was based on a specimen from Sumatra, while two names from Borneo, *T. crassifolia* and *T. montana*, are rightfully treated as synonyms, as in, for example, the *Tree Flora of Sarawak and Sabah*. The name *T. paniculata* 1875 is a synonym of *Tetractomia majus* in the Rutaceae (Dr. Ian Turner, pers. comm.)

A big tree able to exceed one m DBH, with dark brown bark, the leaves are arranged spirally in dense up-

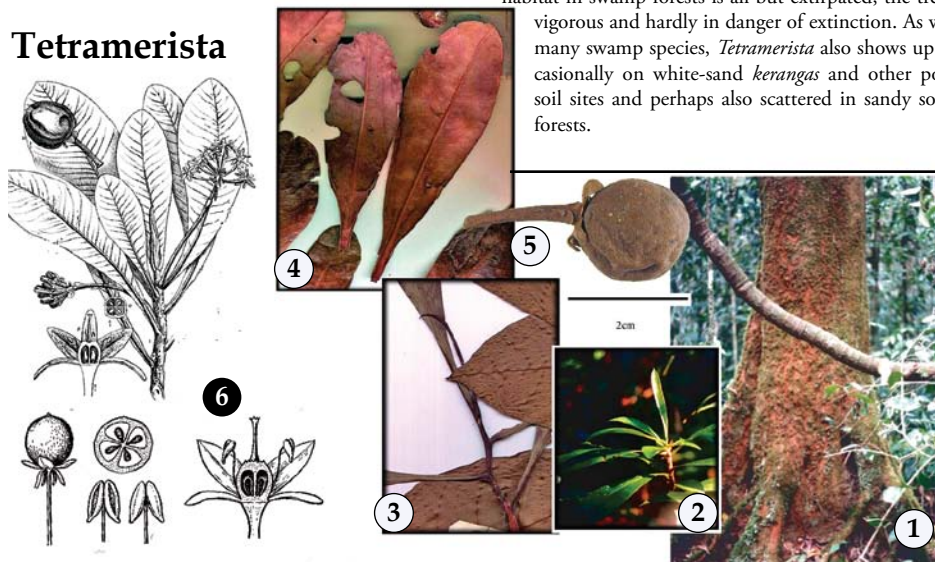
turned clusters; the meristem is hidden within a series of overlapping juvenile leaves that form a characteristic long sinuous apex. The blade is essentially without a clear stalk, rather the leaf joins the stem with a swollen expanded base which continues as a flattened fleshy leaf stalk usually described as winged. The blade surface is shiny, glabrous and bears small black glands below, similar to the small dark pit-glands along the margin. The margin along the lower portion of the blade is decidedly curled, especially when dry. The lower leaf surface dries a distinctive purple-brown color. The main nerves are arched, number about 10-15, hardly lignified, and the veins are obscure, especially when dry.

As the name implies, the flowers are indeed tetramerous, with sepals, petals, stamens, and carpels each numbering four. They are borne on a branched panicle; individual flowers are about two cm across with two persistent bracteoles at the base of the two cm long pedicel; the style 2-2.5 mm long. The fruit is variably 1-3 cm across, crisp and fleshy and bearing four long thin seeds.

A fairly big tree with wide spreading prop-roots, chiefly at home in swamps, especially peat swamps where it is sometimes abundant but typically occurs as large scattered trees with numerous saplings. The juveniles have the odd habit of growing beyond their mechanical capacity of support and falling over to form small thickets of clonal branched offspring, and continuing until death or sufficient sunlight allows for the growth of a more substantial main trunk<sup>1</sup>. Pollination and dispersal are unexplored.

The timber of *Tetramerista* was a negligible product during the last century, but since 2000 it routinely appears in wood markets, especially as flooring. The fruits are said to be eaten in Sumatra. Although the native habitat in swamp forests is all but extirpated, the tree is vigorous and hardly in danger of extinction. As with many swamp species, *Tetramerista* also shows up occasionally on white-sand *kerangas* and other poor-soil sites and perhaps also scattered in sandy soiled forests.

## Tetramerista



*Tetramerista glabra*. 1, the trunk of a large tree in a peat swamp in Borneo; 2, the twig tip of a juvenile; 3, characteristic twig tip and leaf base of dry specimen; 4, the blades dry red, dull, pustulate; 5, dry fruit; (Photographs 1 & 2 © Daniel Gavin; 3 & 4 © Professor Eizi Suzuki; 5, USDA-GRIN public domain image by Robert J. Gibbons; 6, line drawing of leaf, flower and fruit, adapted from *Icones Bogorjensis*, Vol. 4. Plate 83, 1914.)

## BARRINGTONIACEAE

**NAME:** From the genus *Barringtonia*, as below. No common names apply to the family as a whole, but we might call it the *putat* or *cutmut* family. Note that if this family is treated under a broad Lecythidaceae, then the name at the subfamily rank is Planchonioideae.

**OVERVIEW:** The trees of this small family represent a monophyletic group of five genera and maybe 50 species. They fall within the broadly circumscribed Lecythidaceae, a DNA-based monophyly without a morphological synapomorphy, consisting of five clades that are perhaps best treated as five families<sup>1</sup>. The Barringtoniaceae are strictly Paleotropical in distribution and predominantly tropical Asian. They are distinguished by the important if obscure synapomorphy of pollen that is syntriolopate with a thickened colpus ridge. All species in the family are trees although a few are understory plants of the *schopfbaum*-habit, that is, with a single thick stem and a dense rosette of leaves. The flowers are radially symmetrical while the seeds are variably reduced to as few as one. Ecologically, the Barringtoniaceae are of two types. First, are those of the lowland equatorial forest, especially *Barringtonia*, for which a few species are usually abundant in most lowland forests, together with a few *Planchonia* species. Second, are the genera and species of the dry-seasonal forests, which include *Careya*, *Petersianthus*, *Chydenanthus*, and a few species of *Barringtonia*. The family is rare in equatorial mountains; for example, only two species of *Barringtonia* are claimed for Kinabalu.

All are trees with moderately thick twigs, spirally arranged leaves, the blade of which is entire with a strongly serrate margin, or at least a few distant and obscure teeth near the apex. The node is clean. (The paired 'stipules' if they are such, are little more than dark patches.) The twig apex is typical of Ericales with a long thin pointed tip. The flowers are mostly large powder-puffs, bisexual, with a large thick persistent calyx. The radially symmetric flower, nectary disc, long slender style, and few seeded indehiscent fruit collectively distinguish the family from the Neotropical Lecythidaceae.

The genera - all species-poor other than *Barringtonia* - differ most notably from one another in details of the gynoecium, but it would be good to know if *Barringtonia* (with four ovules per locule pendent from the apex, and one mature seed) is monophyletic or if these small genera lie nested within. *Petersianthus* has a winged fruit, while *Chydenanthus* bears an articulated floral stalk, the ovary with one to two ovules from the base. The other three genera all bear numerous ovules arrayed along the axis of the ovary, differing among one another as follows: *Careya* (abundant dry-seasonal) ovules from the axis

midpoint, carpels three, seed arillate; *Planchonia* (common, lowlands of Sundaic Region) likewise, but the mature seed unique in the family in that the embryo bears well-developed plicate cotyledons.

I include in *Barringtonia* the Whitmore genus *Abdulmajidia*, the only distinction being the presence of more than one seed. His genus included two new species, neither known in the field, and each represented by not much more than the type specimens from Maxwell Hill in Perak (*A. maxwelliana*) and Bukit Chini and Gunung Pulai in Johore (*A. chanii*). In 2006, three more species were added<sup>2</sup>. Combinations under *Barringtonia* have not been published.

There is a strong but superficial similarity to those Myrtaceae with spiral leaves while the powder-puff flowers do look like a *Syzygium*. However, in Barringtoniaceae the many stamens of the flower mature from the center of the flower outwards, while in Myrtaceae they mature from the outer edge towards the center.

The economic potential of these trees has been badly neglected. They are sturdy and insect-resistant trees with deep green foliage and attractive night-blooming flowers, and should be far more common in cultivation, both in cities and towns. They could also figure in reforestation. Several have useful timber, and a few bear edible nuts.

**BARRINGTONIA.** [Commemorates Daines Barrington, d. 1800, English naturalist.] The genus is known from Africa to Madagascar, India to Australia and the Pacific. Over 150 basionyms have been published, these represent perhaps 51 species following the last monograph<sup>1</sup>. However, as CORNER *loc. cit.* noted long ago, the variant and localized forms in Asia are not very well resolved. We count about 17 species in Malaya, perhaps 10 species in Indochina, 13 in Brunei, and one species reaches Yunnan in the form of the endemic *B. fusicarpa*. Local names apply to the genus as a whole, although sometimes with additional adjectives for the

## FIELD RECOGNITION

Clean glabrous trees with no exudate.

Leaves of medium to large size in spiral clusters from relatively thick twigs, a candelabra appearance.

Stipules are present, but are a difficult character in that they are greatly reduced or abortive in many species and represented by no more than a tiny bit of black tissue on each side of the leaf base, and only in the youngest leaves.

The leaf blade is usually glabrous, oblanceolate, with small teeth in upper portion (but not in the coastal *B. asiatica*).

The leaf stalk is broadly thickened at the base, typically with two ridges

The twigs are hollow with cortical vascular bundles, which in some genera we find the xylem is to the outside and the phloem to the inside, reversing the normal order.

## FIELD CONFUSION

The general habit of leaf and twig is fairly widespread in Anacardiaceae (e.g., *Camposperma*, but these they have solid twigs, leaf stalk with terete and swollen base, no hint of stipules), a few stalkless pachycaul *Sterculia* (these with 3-nerved leaf), and *Sapotaceae* (these with white exudate).

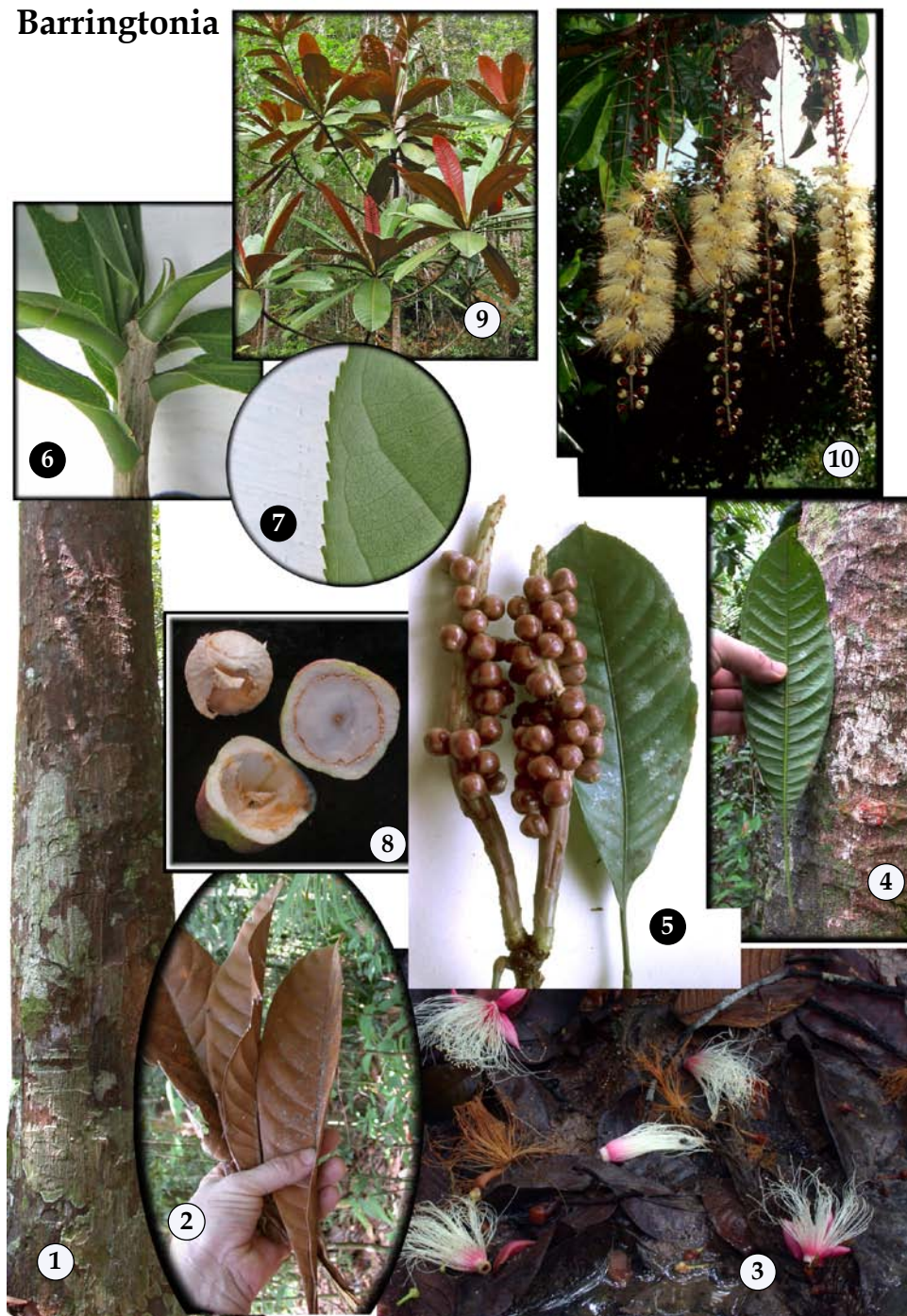
<sup>1</sup>Mori, S. *et al.* 2007. American Journal of Botany. 94: 289-301.

<sup>2</sup>El-Sheriff, I. *et al.* 2006. Folia Malayana 7: 41-54.

<sup>3</sup>Payson, J. 1967. Blumea. 15: 157-263.



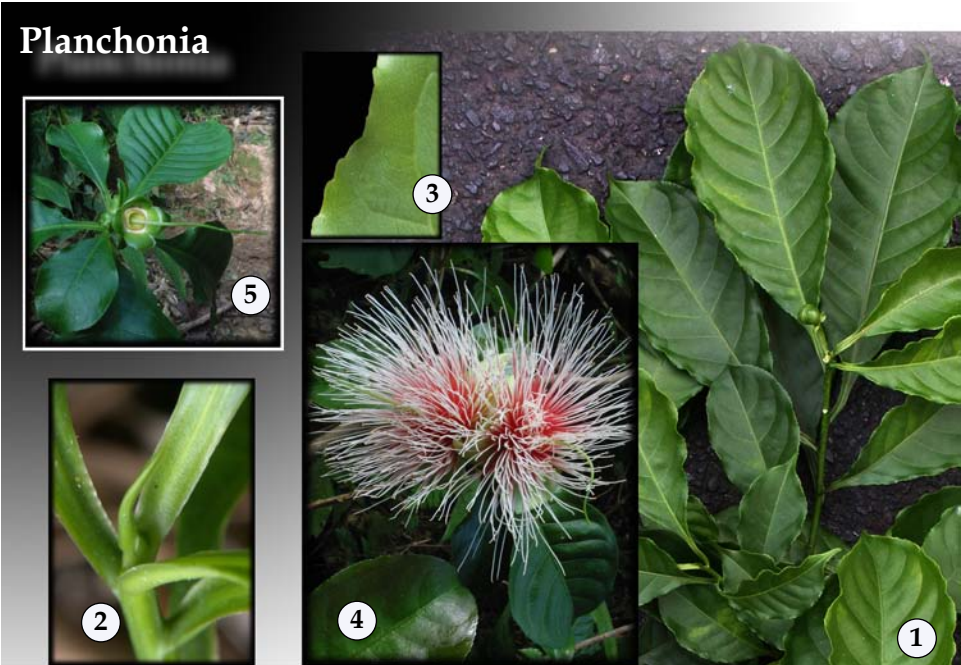
# Barringtonia



*Barringtonia*. 1-2, *B. curranii*, Borneo, 32 cm DBH; 3-5, *B. macrostachya*, Pasoh, Malaya; 3, fallen stamens, 7:30 AM; 4, leaf and flower buds; 5, leaf and bark of mature tree, 16 cm DBH; 6-9, *B. racemosa*; 6, apex with characteristic leaf base; 7, toothed leaf margin; 8, single seeded fruit, thin papery testa, small undifferentiated embryo; 9, from Mt. Hamaguitan, Philippines, typical habit, new leaves red below; 10, *B. procera*, one of the cutnuts, here from Solomon Islands; (Photograph 9, © Leonardo L. Co; 10, © Roger Leakey.)



*Barringtonia asiatica*, from BLANCO *loc. cit.*, plate 305 (as *B. speciosa*). The fruit are about 15 cm across.



*Planchonia spectabilis*, Philippines. 1, leaves loosely spiral and scattered along the twig; 2, twig apex, the stalk weakly differentiated from the blade, flanged; 3, toothed leaf margin; 4, flower; 5, young fruit after stamens fall, calyx lobes and long style persistent. (Photographs 4 & 5 © Leonardo L. Co.)



better known species: *putat* (Malay), *karut* or *langkong* (Iban), *tampalang* (in Sabah).

One or more species of *Barringtonia* can be found in most lowland forests. In general, the most abundant species all have a preference for wet ground. The flowers are often magnificent powder-puffs of white stamens with pink tips and white petals. In most of our species, the flowers inevitably open in the early evening and drop by the late morning at which time you might find them like pink and white tissue scattered beneath the tree. Most all are presumably pollinated by large moths and perhaps bats. However, a group of species bear small red flowers, some open at night and some by day; their pollination remains a mystery.

*Barringtonia asiatica* is an abundant and characteristic tree wherever mature beach forests still remain. The large cork fruits wash up on shores all over the tropical Pacific. The mature tree, while never tall, can exceed one m DBH. It is sometimes cultivated in parks and gardens and should be more widely planted.

A suite of three related species produce edible seeds, the *cut-nut*; all are more or less confined to the vicinity of New Guinea and the Solomons Islands: *B. procera*, *B. edulis*, and *B. novae-hiberniae*. (These are nicely illustrated on the internet. They are remarkable in several respects. The inflorescence is a long pendent spike, sometimes exceeding one m in length; the flowers are exceedingly dense and they bloom slowly over several days,

from the base toward the apex. The seeds are eaten as a supplement or staple food, but only locally. The edibility should be carefully tested because the seeds of *Barringtonia* are so rich in saponins that many species are used as a traditional fish poison.

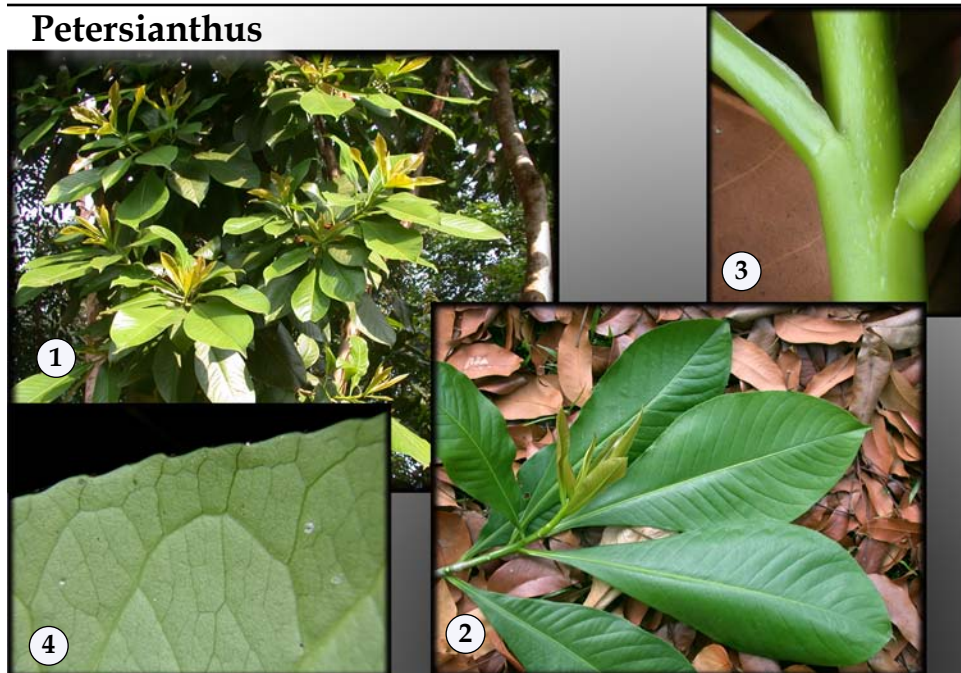
**PLANCHONIA.** [Commemorates Jules Planchon, d. 1888, French botanist, assistant to Hooker at Kew, then professor at Montpellier.] A genus of five species from the Andamans to Philippines and east to Australia. Similar to *Barringtonia* in most regards, but in *Planchonia* the ovules are numerous and attached all along the wall, and the terminal inflorescence is few flowered, whereas in *Barringtonia* the ovules are few, attached close to the top of the ovary chamber, only one (or rarely three) seeds develop, the inflorescence is many flowered elongate, terminal or axillary.

*Planchonia valida* is perhaps the most widespread species. These trees sometimes occur in lowland wet forests, but they are perhaps more abundant in dry-seasonal forests. The Australian species *P. careya* is evidently adapted to frequent ground fires.

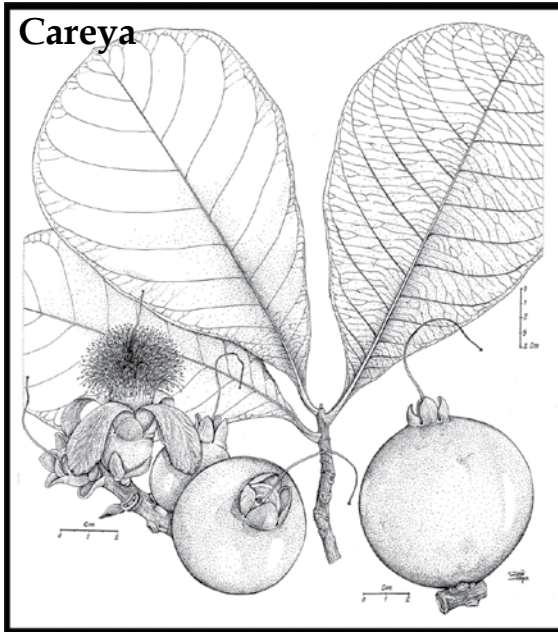
**PETERSIANTHUS.** [Bentham's genus *Petersia* for the African trees is preceded in use by *Petersia* for the Capparaceae; Merrill's new name retains the reference, probably for German botanist C. Peters.] A small genus of peculiar distribution with either one or two species in west Africa, especially *P. macrocarpus* as a large timber

Traditional Trees. (<http://www.traditionaltrees.org/>)

## Petersianthus



*Petersianthus quadrilatus*. 1-4, cultivated at Mt. Makiling, Luzon, Philippines. 1, upturned spiral clusters of leaves, young leaves reddish green; 2, blade with strong regular nerves, arched and closed at the margin; 3, clean node, the stalk weakly differentiated from the blade, with laminar flange; 4, toothed leaf margin.



*Careya arborea*, adapted from BUNYAVEJCHEWIN *loc. cit.*

tree that is also an important nesting site for African hornbills. The second main species is found only in the south central islands of the Philippines, *Petersianthus quadrialatus*. The tree is distinguished by the more or less four-winged fruit, terminal inflorescence and four-celled ovary with numerous axile ovules. This is a very large tree. Merrill's original description cites a cut tree measuring 182 cm DBH at two m above the buttresses. It is locally well-known in Samar where the tree is called *toog*, the timber sometimes as *bayong*. The species was planted by the US foresters at Los Banos Luzon at the start of the 20th century where the trees now exceed 80 cm DBH, but otherwise this interesting species has not attracted the attention that it deserves. It merits further cultivation and study of plantation use.

**CAREYA.** [Commemorates Baptist missionary Rev. W. Carey, d. 1834, British plant collector, founder of Serampore Botanic Gardens, translator of Bible to Hindi.] A genus of four species. *Careya arborea* is abundant in the strongly seasonal forests and ruderal habitats of Indo-Burma, barely reaching Malaya. It is an especially common tree in the dry-dipterocarp forests of Mainland SE Asia, and can withstand repeated ground fires. In Sri Lanka, it is often the only tree species persisting in the *patanas* grasslands. It bears more than one seed per fruit. The seeds sometimes considered edible.

*Careya sphaerica* is known from Thailand, Laos, Cambodia and Vietnam, sparsely found in most of the varied forest types below 1000 m. The tree demands strong light during establishment. It is usually found on arid, acidic, periodically inundated soils. The flowers are said to have a stronger and more unpleasant odor than typical in Barringtoniaceae.

**CHYDENANTHUS.** [Greek, abundant flowers.] Probably monotypic, *Chydenanthus excelsus*, distinguished by the ovules which are few as in *Barringtonia*, but attached near the base of the floral axis; the floral stalk is jointed. This is a poorly known species, most often a small tree although some herbarium labels report a height of 30 m. It found in seasonally dry places from Myanmar to Sumatra, Java and Bali, and possible in east Borneo.



*Chydenanthus excelsus*, as illustrated in the original transfer of *Barringtonia excelsa* by Miens in the Transactions of the Linnean Society, Botany series 2. 1: 111 (1875).



## OTHER ASTERIDS: ERICALES

## SAPOTACEAE

**NAME:** Sapotaceae is an old and traditional name derived from the Aztec *xapote* for *Pouteria sapota*. There is no modern genus *Sapota* and the name has nothing to do with sap although most members do in fact exude white latex. Throughout the Malay world these trees are known by the timber name, *nyatob*. Singular names are given to the exotic cultivated species and perhaps also to a few abundant local species; local names do not conform to genera.

**OVERVIEW:** A pantropical family of 53 genera and 1100 species. In tropical Asia we find 13 genera and about 250 species. The family is readily recognized in the field from the features noted under Field Recognition. Some widespread species, such as *Payena lucida*, *Mimusops elengi*, and *Palaquium kingii*, are distinctive and easily recognized, as are many rare species such as *Palaquium clarkeanum* or *Palaquium beccarianum*. The genera, however, are notoriously ambiguous and there are no field characters by which to place an unrecognized Sapotaceae in the correct genus. *Index Kewensis* lists over 5000 names in the Sapotaceae and nearly 300 published genera. The analysis by Pennington<sup>1,2</sup> sensibly reduced that chaos to 1100 species and 55 genera by emphasizing the details of calyx, corolla and stamen, especially the number of parts and their relative position. However, these are the very characters that molecular studies have shown to be highly pleiomorphic in the Sapotaceae, and indeed across the entire Ericales. It was little surprise when the first molecular studies proposed a substantial reorganization<sup>3,4</sup>. The rearrangement continues today, some of our genera are lumped while others are divided.

The principle findings of the molecular studies are as follows. *Sarcosperma* is placed in its own subfamily and is sister to the rest of the family which divides between two large clades, the Sapotoideae and the Chrysophylloideae. Most of our regional Sapotaceae, especially those of the lowland equatorial forest, fall in the former. A study aimed specifically at the Sapotoideae found that *Engelhardtia* must be withdrawn and placed sister to the two large subfamilies, leaving it outside the three subfamily arrangement for the time being<sup>5</sup>. The other genera of the Sapotoideae are weakly resolved and the sampling of the large genera *Madhuca* and *Palaquium*, so important



A fallen fruit of a species of *Madhuca* from Pasoh, Malaya, well-known at the site, but as yet without a name and possibly new. The fruit is about 4 cm across and reveals the shiny brown seeds with the long scar typical of the family.

in the Asian region, was too sparse to reach conclusions with regard to monophyly. Within the *Chrysophyllum* subfamily, the genus *Pouteria* when broadly conceived is polyphyletic; studies based on Australian and New Caledonian species have clarified the main clades within this group and recommended the resurrection of *Beccariella*, *Planchonella*, *Sersalisia* and *Vanroyena*, of which only *Planchonella* falls within our region<sup>6,7,8</sup>.

The flowers of Sapotaceae are of the Ericalean type, that is, radially symmetric, 5-10 mm across with dis-

## FIELD RECOGNITION: SAPOTACEAE

Trees, large or small, the big trees usually develop a warm red-brown bark with shallow fissures, sometimes scaly, rarely smooth.

Pure white exudate is always present in the twig and slash.

The leaves are simple, often obovate or with a tapered base and are most often arranged in dense upturned clusters; many species have twigs that seem disproportionately large for the leaves.

The leaf stalk is often tapered from base to apex

Stipules always present, but usually quickly fall off without leaving a noticeable scar

Red hairs and gold scales are common on the lower surface of many species.

Naked terminal buds with adpressed, brownish, often T-shaped unicellular hairs,

Axillary branches often with prominent, basal prophyllar buds and then long internodes,

## FIELD CONFUSION

The dry leaves of some Anacardiaceae might be confused in that they share with Sapotaceae a tapered leaf stalk, and the scale leaves might be mistaken for stipules; however, Anacards have black or clear resin.

<sup>1</sup>Pennington, T. 1991. The Genera of Sapotaceae. Royal Botanical Gardens.

<sup>2</sup>Pennington, T. 2004. The Families and Genera of Vascular Plants. 6: 390-421.

<sup>3</sup>Andenberg, A. et al. 2003. International Journal of Plant Science 164: 763-773.

<sup>4</sup>Swenson, U. et al. 2005. Cladistics 21: 101-130.

<sup>5</sup>Smedmark, J. et al. 2006. Molecular Phylogenetics and Evolution. 39: 706-721.

<sup>6</sup>Swenson, U. et al. 2007. Cladistics 23: 201-228.

<sup>7</sup>Swenson, U. et al. 2007. Taxon. 56: 329-354.

<sup>8</sup>Triono, T. et al. 2007. Australian Systematic Botany 20: 107-118.



A large tree, over 80 cm DBH, of *Pouteria dulciana*, Mt. Makiling, Luzon, Philippines.

tinct calyx and corolla, the latter at least weakly fused, while the stamens are typically fused to the petal base or densely clustered and fused in the upper throat. The petals and anthers typically fall as a unit; the ovary is of several untied carpels and bears a pointed style. The calyx varies most critically among genera with two main types: (1) the calyx in a single whorl, variable in number, often with overlapping edges; (2) the calyx in two series, the outer essentially valvate, often of two calyx members that enclose the flower in bud, while the inner whorl is variable. The number of calyx lobes, petal lobes, and



A wood sample of *nyatoh*, unidentified to species, from the Sarawak Timber council, showing the characteristic straight grain and red color.

stamens are often doubled or reduced forming varying numbers of series. The most characteristic reproductive feature of the family lies in the fruit, which develops from one to 30 carpels, each with one ovule attached to a more or less incomplete central axis that may be reduced to little more than a stump, and so render the attachment basal, but an attachment that almost always leads to a characteristic scar on the seed (the hilum) which is otherwise thick, shiny and brown.

The Sapotaceae are an easy family with which to get started. The field characters are decisive, obvious and reliable, and the cultivated species - *chiku*, star-apple, *Mimusops* - readily provide examples of flowers and fruit. Furthermore, reasonably complete taxonomic treatments exist for much of the region, and even sterile leaves can sometimes be matched to annotated type specimens. However, a start is usually all anyone can ever make. Most of the 250 species of Sapotaceae in tropi-



Different patterns of venation within the Sapotaceae are usually diagnostic only to species and can vary among the larger genera.

The Genera of Sapotaceae in Tropical Asia

GENUS	KEY FEATURES	DISTRIBUTION
Sarcospermatoideae		
<i>Sarcosperma</i>	Leaves roughly opposite, nerves with axillary pits, some species stipels at junction leaf stalk and leaf base; inflorescence an open panicle.	8 species, widely in Asia.
Unplaced		
<i>Eberhardtia</i>	Sepals 4-5 in 1 whorl, corolla with appendages, fruit a dehiscent capsule, fruit wall strongly constricted between the several seeds.	3 species, China, Vietnam, east Borneo, rare, montane.
Sapotoideae		
<i>Palaquium</i>	Sepals 6 in 2 whorls, corolla without appendages, stamens 12 stamens, staminodes 0.	100 species, widely in tropical Asia.
<i>Madhuca</i>	Sepals of 2 pairs, corolla lobes 6-17, hairy throat, stamens 12-43 in several whorls, exerted, style often very long, exerted, fruit 1-seeded.	100 species, China to Australia.
<i>Aulandra</i>	Sepals 4-5, 1 whorl.	2 species, endemic to Borneo.
<i>Isonandra</i>	Sepals 4-5, imbricate, 2 imperfect whorls, corolla 4-5 lobed, glabrous tube, 8 stamens, 4-5 locular ovary, fruit 1-seeded.	10 species, tropical Asia
<i>Diploknema</i>	Stipules much reduced, sometimes dioecious, sepals 4-5 in 1 whorl, 6-15 locular, otherwise as in <i>Madhuca</i> .	10 species, tropical Asia.
<i>Payena</i>	Distichous alternate leaves with single irrigating vein; flower and fruit as in <i>Madhuca</i> although corolla tube usually glabrous within.	About 20 species, tropical Asia, abundant small trees.
<i>Mimusops</i>	Sepals 4 in 2 whorls, corolla 8 lobes, each divided into 3, stamens 8, seed with small circular scar.	30 species, Africa and eastward, 1 cultivated and probably adventive in tropical Asia.
<i>Manilkara</i>	Sepals 6 in 2 whorls, with corolla appendages, sometimes 6, and staminodes, long seed scar.	80 species, pantropical, 10 in tropical Asia, 1 exotic cultivated.
<i>Sideroxylon</i>	Sepals 4-5, 1 whorl.	80 species, America, Africa, Indian Ocean and Pacific, not Borneo.
Chrysophylloideae		
<i>Xantolis</i>	Branch spines, sepals 4-5, 1 whorl, hairy filaments.	14 species in dry seasonal tropical Asia.
<i>Chrysophyllum</i>	Without stipules, sepals 4-5 in 1 whorl, corolla and stamens usually equal in number to sepals.	70 species, pantropical. 1 from India to Borneo, <i>C. roxburghii</i> and 3 cultivated.
<i>Pouteria</i>	Sepals 4-5, 1 whorl, fruit > 2.5, long broad lateral seed scar.	200 species, tropical America, a few elsewhere; maybe 20 in tropical Asia.
<i>Planchonella</i>		65,

cal Asia are genuinely rare, living at low densities, often geographically restricted, and so it is difficult to get know the individual species. Of the 47 species of *Madhuca* recorded for Sabah and Sarawak, more than half are noted as “rare, uncommon, known only from a few collections.” Because of the rarity and difficulties of field recognition, it is unlikely that there will ever be a Symington for the Sapotaceae, that is, someone to walk the

forest and learn all the species and masterfully blend that field knowledge with a critical review of the herbarium specimens.

The Saptoceae are not the largest of trees, but many species exceed 60 cm DBH in maximum size, and a few are fairly tall. However, the majority of species reach maturity between 10 and 20 cm DBH, and a few never ex-



ceed 10 cm. Growth rates of forest-grown species reach the relatively fast rates of 0.5 cm per year.

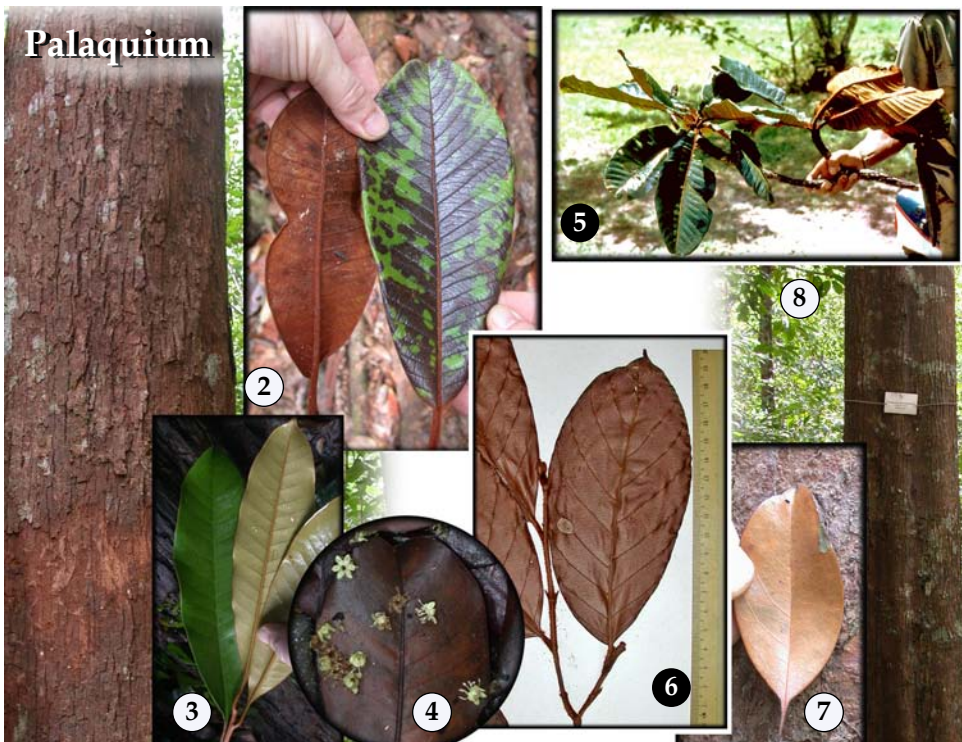
Perhaps more than any other major tree families, the Sapotaceae show strong species specificity with regard to distribution over soil richness, some species found preferentially over nutrient-rich shale and clay soils, others restricted to nutrient-poor sandstone soils. All 32 species of Sapotaceae at Lambir, Sarawak, showed some degree of soil specificity with varying additional preferences for ridges or valleys.

The introduced *chiku* and *Mimusops* flower more or less all the time. Other species produce flower buds and then have a long-delayed period before they open more or less in synchrony. The flowers of many species are odd in hanging downward; more than a few may be pollinated by bats or small tree-climbing rodents that eat the corolla.

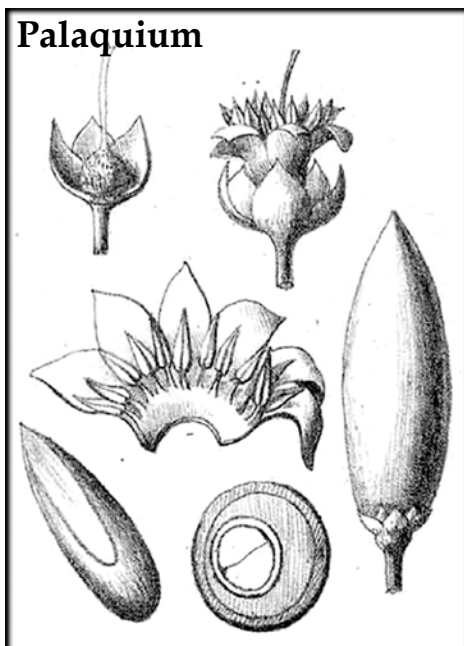
All of the trees that reach at least 30 cm DBH are exploited for timber, without any discrimination to species. Two classes of timber are recognized: the most abundant is a light and easily worked wood that is sold as *nyatoh* while those species with a hard heavy timber are classed as *nyatoh temiang* or *bitis*.

Of the native species, the main cultivated tree is *Mimusops elengi* which is grown everywhere for shade, fragrant flowers, decoration, a hard decorative wood

and medicine. It is popular in cities owing to its ease of growth and strong resistance to urban abuse. *Palaquium gutta* was once the basis of a local plantation industry which left residual stands of trees here and there, most obviously in Singapore around the margins of Bukit Timah. Otherwise, our three main cultivated fruit trees all originated in America. *Achras zapota* was brought in early days to the Philippines from Mexico, but the name that followed was not the Aztec *zapote* nor the widely applied *sapodilla*, but *chico* which in Malaysia became *chiku*. It is a hardy and long-lived tree that remains popular around older village homes everywhere. *Pouteria sapota* is also of Mexican origin and is widely if sparsely still grown in Luzon under the name *mamei*. The most abundantly planted Sapotaceae is also the most recent introduction, *Chrysophyllum cainito*, the star apple which only appeared in the Philippines in the 19th century and is sparsely planted in Malaysia and Indonesia. The name should not to be confused with the unrelated star fruit. Our native species are edible in that they are evidently not poisonous, but they are generally regarded as insipid.



*Palaquium*. 1-2, *P. beccarianum*, Lambir Sarawak, the warm red bark typical of the family, the leaf is distinctive to species in the dense red felt below and strong looped nerves; 3-4, *P. gutta*, Singapore, with coppery golden lower surface; when in bloom the fallen corollas litter the ground; 5, the rare *P. clarkeanum*, Pasoh, Malaya, note the thick twigs, *Terminalia*-habit, and feltish red lower surface; 6, *P. dasyphyllum*, Lambir, Sarawak, with alternate leaves, red hairy surface and twigs, narrow scalariform veins; 7, *P. microphyllum*, Singapore, a typical trunk for Sapotaceae, but here with a very small leaf.



Floral details of *Palaquium philippense*. (Illustration adapted from VIDAL *loc. cit.*, plate 52, as *P. latifolium*).



*Palaquium elegans*, a herbarium specimen from Lambir, Sarawak; a small tree with a remarkably narrow distribution over wet shale soils.

### ❧ - Sarcospermatoidae - ❧

**SARCOSPERMA.** [Greek, fleshy seed.]. Between six and eight species, from the Himalayas and S China to Mainland SE Asia, then, the relatively uncommon *Sarcosperma paniculatum*, sparsely from the Malay Peninsula to the rest of tropical Asia and New Guinea, but not in the Philippines. Distinctive in the family in that the leaves are more or less opposite - but see spiral leaves in *Sarcosperma laurinum* illustrated in THROWER *loc. cit.* The node includes odd stipels on the leaf stalk at the base of the blade and pit glands in the nerve axils of the blade. Unlike other Sapotaceae, the inflorescence is an extended raceme or panicle.

### ❧ - Unplaced - ❧

**EBERHARDTIA.** [Commemorates A. Eberhardt, German botanist.] An enigmatic genus of three species, only one of which is widespread *Eberhardtia aurata*. Principally a genus of S China and Mainland SE Asia with *E. aurata* represented by three recent collection in E Sabah. Evidently, it is mainly found in montane forests with a strong dry season. Certainly when sterile it would be overlooked as an unidentified Sapotaceae, and only when bearing its peculiar ribbed fruit might you notice its excentricity. The flower is also peculiar in that the lobes of the petals bear two membranous appendages on the back and the five stamens are joined by five staminodes, longer than stamens and each with an abor-

tive anther that forms a spear-shaped appendage. (Not illustrated.)

### ❧ - Sapotoideae - ❧

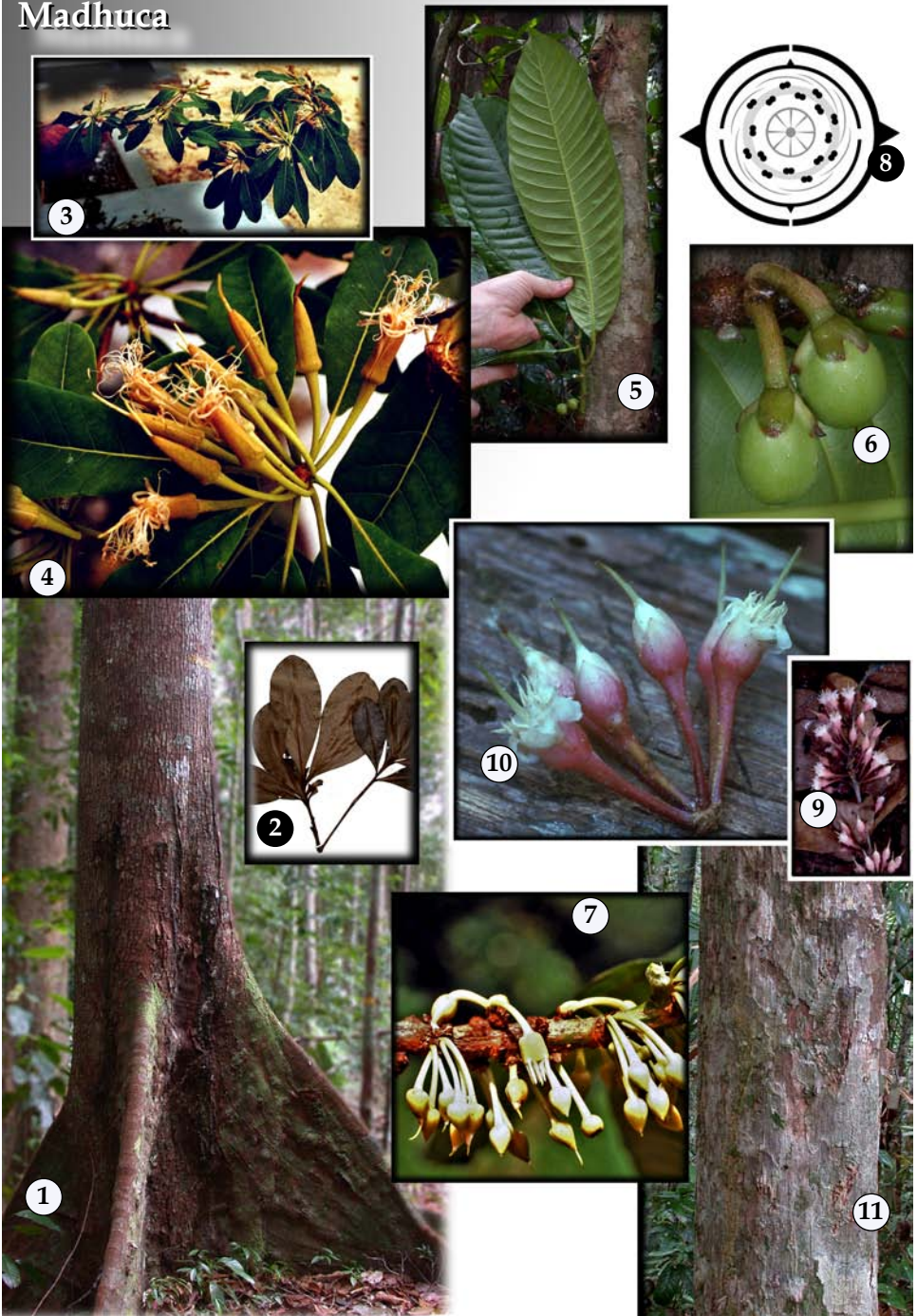
**PALAQIUM.** [From the Philippine vernacular *palak-palak*.] A species-rich genus with many local and uncommon species, perhaps 110 species in total, from India to the Pacific, especially Borneo (50 species) and the Philippines (29 species). The venation is often closely scalariform, although the details overlap with other genera.

Although many species of Sapotaceae can be tapped for the white latex, *Palaquium gutta* is historically the most important. The industry began in the 18th century, was greatly stimulated by the need for rubber coated undersea cables in the late 19th century, and reached a peak in 1930s before collapsing in the face of industrial substitutes. The latex was collected destructively by felling the entire tree. By 1847, Thomas Oxley estimated that nearly 70,000 large trees were cut every year in Malaya to provide gutta-percha. Plantings of *P. gutta* began in the early decades of the 20th century and by 1930 Malaya included about 300,000 ha of 'gutta-percha forests'. See BURKILL *loc. cit.* for further details.

Although most species are exceedingly uncommon, a few species are frequent in the region and patchily abundant. *Palaquium regina-montium* is gregarious in many Malayan hill stations; *P. obovatum* is likewise frequent in lowland and lower hill forests from Indochina to Borneo.



# Madhuca



*Madhuca*. 1-2, *M. sessilis*, Lambir, Sarawak, the trunk with red bark and low narrow buttresses is typical of the family, the leaves are arranged in spiral clusters; 3-4, *M. crassipes*, Lambir, Sarawak, note the *Terminalia*-habit, the paired calyx lobes tightly closed; 5-7, *M. malaccensis*, Pasoh, Malaya, flower and fruit; 8, floral diagram illustrating the basic organization of flowers in *Madhuca* as described in the text; 9-10, an inflorescence and floral cluster from a species of *Madhuca* from Pasoh, Malaya, as yet unnamed, possibly new, (noted in the 50-ha plot as "*Ganua* sp. 1"); 11, *M. pallida*, Lambir, Sarawak, 32 cm DBH, a flaky gray-red bark, the trunk unbuttressed;





*Madhuca pierrei* from lowland forest in southern Vietnam, the red bark, white exudate; the ground densely littered with fallen yellow corollas, a fallen twig with dried flowers, and the large leaf, with loose open reticulate venation.

**MADHUCA.** [From the Indian name for *Madhuca longifolia*, the seeds of which used for oil.] A large genus that might best include *Ganua*. In present conception, *Madhuca* includes at least 100 species, distributed from India to Indochina, to Borneo (50 species), Philippines (12 species) and Australia. Leaf venation is mostly reticulate, but the genus overlaps with others in vegetative features.

**AULANDRA.** [Greek, furrowed-anther, reference to the staminal tube.] A small genus of three species restricted to Borneo. Essentially a *Palaquium* but with the stamens fused into a staminal tube. (Not illustrated.)

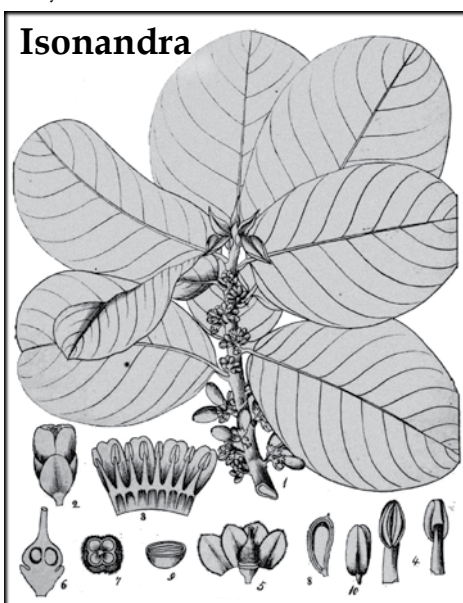
**ISONANDRA.** [Greek, equal anthers.] An old genus name now applied to about 10 species distributed from S India and Sri Lanka to Borneo, with only *I. perakensis* on limestone in N Malaya, two uncommon species in Borneo. Roughly a *Palaquium* but the corolla with four-lobes, the stamens eight, the ovary with four locules. The fruit is similar to *Burckella*, a genus with 14 species distributed chiefly in the Pacific with *B. obovata* important in New Guinea.

**DIPLOKNEMA.** [Greek, two spikes or points, unclear reference.]. 10, species chiefly of the strongly dry seasonal forests, from India to S China but only *D. sebifera* to N Malaya (twice collected) and Borneo (Sabah,

Kalmantan) and New Guinea, and *D. ramiflora* in Northern Luzon Philippines, with almost certainly additional species in Palawan and western Mindanao. The genus probably should include *Aesandra*, the latter of two species from Indochina, the ovary with 12 locules and five-six seeds.

**PAYENA.** [Commemorates French chemist Anselme Payen, d. 1871, described structure of cellulose, etc.] A distinctive genus of 15 species, from the Andamans and Mainland SE Asia to Borneo, especially abundant in the lowland equatorial forests of the Sundaic Region. Only *Payena leerii*, north into Mindanao and southern Philippine Islands. Recognizable by the leaves more or less alternate in a plane, and by the nerves, widely spaced and looped with a single branched vein within.

The flower is close to *Madhuca*, two + two sepals, eight petals, 16 stamens, eight locules, abundant albumen versus scant in *Madhuca*, and a broad scar versus a narrow scar in *Madhuca*. The Indochinese species of *Madhuca* approach *Payena* most closely.



*Isonandra villosa*, an Indian species but showing the characteristic floral form of 4 calyx lobes in 1 whorl, a 5-lobed corolla tube with 8 stamens, and a 4-celled ovary. (Adapted from WIGHT *loc. cit.* Vol. 3, plate 360).

**MANILKARA.** [From a South Indian or Malabar name.] A pantropical genus of 65 species, 15 in Asia and Pacific, 20 in Africa & Madagascar 20, and 30 in America. Poorly represented in our regional flora, with no native species in Malaya or Borneo. Indochinese species include the relatively well-known *Manilkara kauki*, cultivated for the fruit. *Manilkara fasciculata* is fairly common in Indonesia and into new Guinea, Sulawesi and north in the wet eastern forest of Mindanao and Samar of the Philippines.

The best known species is *Manilkara zapota*, (with much literature under the synonym *Achras sapota*). The best known local name is *chiku*, but variously also as *zapote*, *chiko*, and *buah menila*. A Mexican tree brought to the Philippines by Spaniards centuries ago and now widespread. The fruit is delicate, sweet, but lacking acid and so a bit cloying. The white gums give a chicle that was sought after in times past.

**MIMUSOPS.** [A Linnaean name, unclear, from Greek or Latin for mimic and look alike, in some reference to the similarity to other Sapotaceae.] Basically an African genus. 30 species, but *Mimusops elengi* native at least to India. In our region it is chiefly as a cultivated tree of cities and parks. Variable forms of this tree are found growing in open forests in the dry seasonal parts of tropica Asia - some of them distinguished under the names *M. arvifolia*, *M. javanica* and so on - but these are now broadly synonymized under the Linnaean name. These may well be naturalized from cultivated populations brought from India long ago.



*Payena maingayi*, Pasoh Malaya; the alternate leaves (10-15 cm long) and leaf venation is distinctive to the genus.



*Mimusops elengi*, is easily recognized by the bright green leaves of distinctive venation, white sap and pendent bright red fruit; the cultivated forms of tropical Asia, here along a roadside in Vietnam, are probably from India.



*Chrysophyllum roxburghii*, the twig about 40 cm long, the small regular leaves are alternate in a plane; axillary clusters of small stalked flowers; drawn from the type specimens.



## Xantolis



*Xantolis*. On the left, *X. tomentosa*, and Indian species, with details of the flower and fruit; on the right, *X. cambodiana*, on coastal hills in central Vietnam, one of the driest places in tropical Asia; note the branch thorns. (Illustration from ROXBURGH *loc. cit.*, Volume 1, plate 27.)

## Pouteria



*Pouteria firma*, (= *Planchonella firma*) to the left, in fruit at Palau, Philippines; to the right, in flower in Mingan, Philippines. (Photograph on left, © Leonardo L. Co; photograph on right, © Ulysses Ferreras.)



**SIDEROXYLON.** [Greek, hard wood.] The current view of the genus is one of about 50 species in the American tropics, and about 25 in Africa, Madagascar, N India to Yunnan, perhaps two rarely in Mainland SE Asia. (including *Sinosideroxylon*). However, note that the genus name, which is an old Linnaean name, has been widely applied in the past to all sorts of Sapotaceae. The trees bear simple open cup-shaped flowers, each with five sepals, five spreading petals shortly fused at the base, five stamens fused to the corolla opposite the petals with five staminodes alternate. The seed bears a basal circular scar and the embryo is sometimes vertical. Two uncommon species are the rarely collected *Sideroxylon harmandii* from the Mekong and *S. wightianum* of the Himalayas to Yunnan and at least northern Vietnam (illustrated in the *Flora of China*). Also in the genus is *S. sessiliflorum* in Mauritius, which is commonly said to have been obligately dispersed by the now extinct dodo.

### ❧ - Chrysophylloideae - ❧

**XANTOLIS.** [Rafinesque name, probably from a native name.]. 14 species distributed from S India to Indochina (six species) but it is not in Malaya nor in Borneo. In the Philippines, a single species, *Xantholis parvifolia*, is found along the strongly dry seasonal west coast of northern Luzon. Several species are found in Mainland SE Asia; most are quickly distinguished by the stout thorns on the branches and trunk.

**CHRYSOPHYLLUM.** [Greek, golden-leaf, in reference to the color on the lower surface of some species.] A genus of 70 species, 43 American, 15 African, 10 Madagascan, only two or three from India to Australia. The most common native species is probably *Chrysophyllum roxburghianum*, a tree of medium stature with numerous small leaves arrayed alternately along the thin twigs. The venation of the blade is closely parallel. This species looks very different from the cultivated star apple, *Chrysophyllum cainito*. This familiar village tree with an origin in the Neotropics has leaves that are deep green above and copper below.

**POUTERIA.** [From a native name of Guiana.] A large and unsatisfactory genus with a name that has been applied with great breadth and heterogeneity. IPNI lists over 600 combinations under *Pouteria*. Most of the diversity lies in the S America where *Pouteria* is represented by many abundant species, many fruit and timber trees. The tropical Asian representatives are a heterogeneous group, uncommon over most of the region, but more abundant and diverse between Borneo and Australia. In the past, many genera were lumped within *Pouteria* and four of these (*Beccariella*, *Planchonella*, *Sersalisia* and *Vanroyena*) are now to be resurrected as a result of molecular studies. The most common species in our region include *P. obovata*, (*Planchonella obovata*) a small tree of sandy shores, and *P. firma* (*Planchonella firma*) of lowlands and lower hill forests.



Cultivated fruits of the Sapotaceae, all three shown here are of American origin. 1, *Manilkara zapota* widely known as *chiku*; 2, *Pouteria sapota*, chiefly in the Philippines, known as *mamei*, the seed with the characteristic scar diagnostic for the family; 3-4, *Chrysophyllum cainito*, star apple, fruit with numerous locule; in flower, note the golden lower leaf surface and open sprays of small flower. (Photograph 4, © Leonardo L. Co.)

## OTHER ASTERIDS: ERICALES

## EBENACEAE

**NAME:** In English, this is the persimmon or ebony family and chiefly comprises species of the genus *Diospyros*. Common sense would suggest that the family name should be Diospyraceae, a name in use since the 18th century and validly published as early as 1818. The competing name, Ebenaceae, is also of ancient and common use with a meaning of 'trees that produce ebony' in the way that Guttiferae means 'sap bearing'. Note that Ebenaceae does not include the genus *Ebenus*, which is the valid name of an African legume. Although Ebenaceae was validly published at the late date of 1891, the family name was conserved under the ICBN, and the logical and earlier name Diospyraceae is not currently allowed as an alternative. Local names are given under the genus heading.

**OVERVIEW:** About 500 species are expected with further collecting. The understanding of lineages within the family has been clarified recently<sup>1</sup> and the presentation here reflects these findings. The family is strongly monophyletic and includes four strongly monophyletic genera: *Lissocarpa* (eight species) in S America, two genera in southern Africa, *Euclea* (20 species) and *Royena* (20 species), and *Diospyros* with maybe 450 species.

**DIOSPYROS.** [Greek, seeds of the gods.] Local names apply broadly to the genus, or in a few cases to particular kinds of *Diospyros*. Most make some reference to the characteristic black bark: Malay is *kayu arang*, Iban *kayu malam*. In the Philippines, *kamagong pil* for the timber, *mabolo* is the fruit of *D. blancoi*.

The current view of the genus reckons about 450 species worldwide with special richness in tropical Asia where we find perhaps 180 species, and also Africa and Madagascar. More than a dozen strong clades were found within the genus, none yet named but all contrary to traditional subgeneric classifications. A few species are found in the warmer parts of the Temperate Zones of Asia and America, and a few species are known from the American tropics. Although the last regional monograph is old<sup>2</sup>, most of the constituent parts of tropical Asia have recent reviews of their species. We find 64 species in Malaya, 75 in Sabah and Sarawak, and 38 in the Philippines. Local richness can be very high with 27 species counted for Kinabalu, 25 in the 50-ha plot at Pasoh Forest, Malaya and 35 at the 52-ha plot at Lambir Hills, Sarawak.

These are dioecious trees and shrubs; sex change has been seen a few times in a few different species. The flowers of the different species are generally similar to one another: the flowers are small with parts in threes or fours,



The cultivated persimmon, *Diospyros kaki*, illustrates the 4-part persistent calyx and the internal form of the fruit, although the soft flesh and seedless condition are not typical of the genus. In the background is the tree which is extensively cultivated in some highlands of tropical Asia, especially as shown here in the Central Highlands of Vietnam.

FIELD RECOGNITION: *DIOSPYROS*

Small or large trees, bark typically black, hard and silicate, scrapes like glass; the twigs quickly turn from glossy green to dark black; a thin black inner layer is revealed by a small cut. The inner bark itself is typically yellowish, darkens rapidly, the live wood is typically very white, without exudate or odor.

The horizontal branches arrayed in wagon-wheel fashion.

Eah twig is a units of episodic growth interrupted by a resting bud that aborts and is continued by an axillary bud.

The leaves along each twig increase in size from the distal to proximal end, sometimes with the final leaf again of smaller size.

The pith in young twigs is soft and septate; the twig bark is held tightly to the wood, never peeling with a fish-net fibers below, as in Annonaceae.

Leaves are simple, alternate along horizontal branches, from short unswollen leaf stalks, elliptic blade with entire margin, nervation (if visible) ordinary pinnate, no stipule, no odor.

The blade almost always bears some black or yellow dot glands, near the stalk or scattered and always of the laminar type, never a raised cup.

The midrib is often raised above which would distinguish many ebonyes from most of the regional trees in Annonaceae.

## FIELD CONFUSION

The wagon-wheel branching is similar to the nutmegs, Myristicaceae, some of which also have a coal-black bark, but the nutmegs have red sap in the bole.

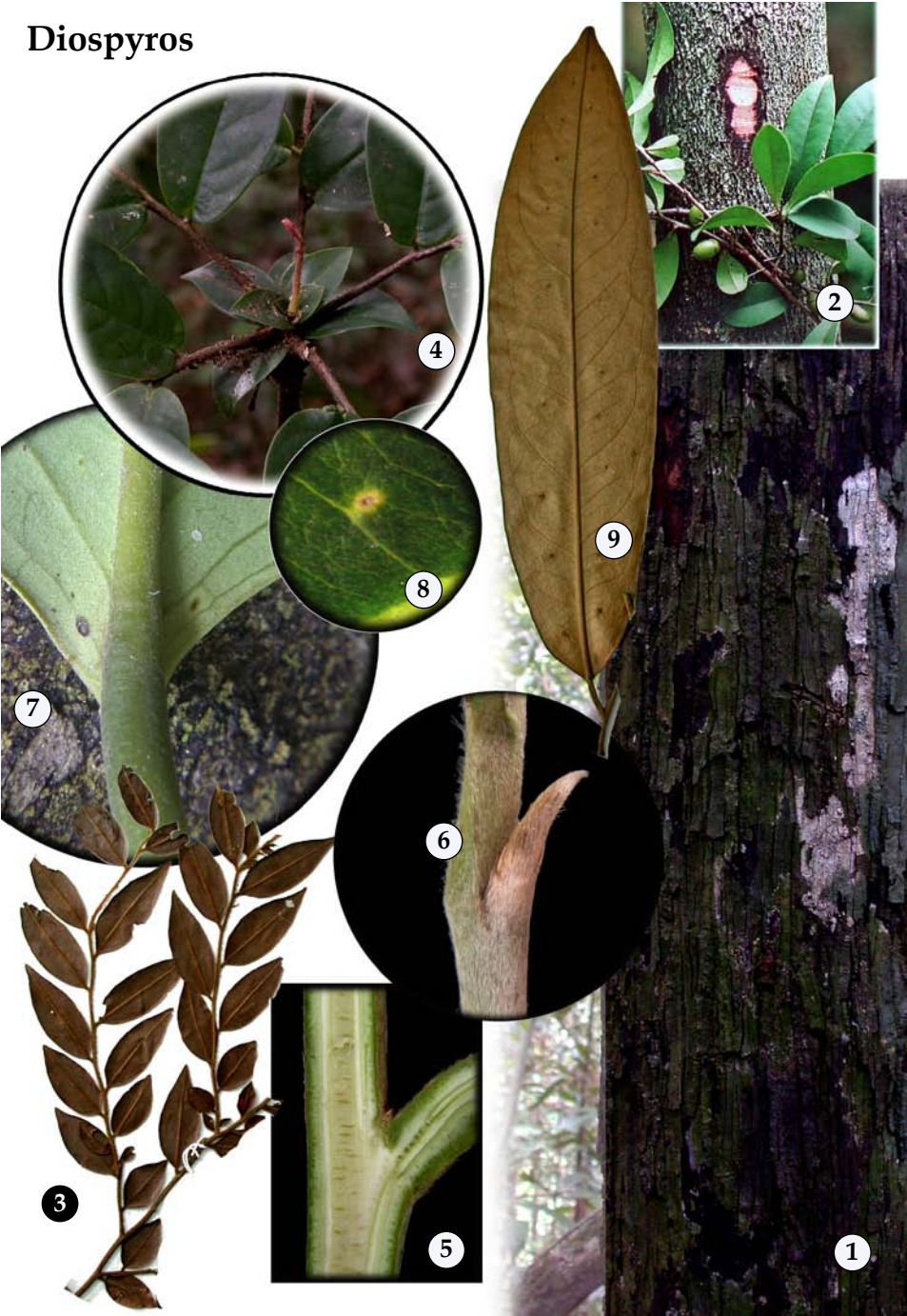
From *Xanthophyllum* by the green twigs, oily odor and warty soft yellow bark, the branches not in whorls.

Saplings of the small-leaved *D. buxifolia* can be confused with *Anisophyllea disticha* which shares a wagon-wheel branching, but note the small anisophyllous leaflets at each node.

<sup>1</sup>Duangjai, S. 2006. American Journal of Botany. 93: 1808–1827.

<sup>2</sup>Bakhuizen van den Brink, R. 1936–1955. Bulletin du Jardin Botanique de Buitenzorg, 15: 1–515.

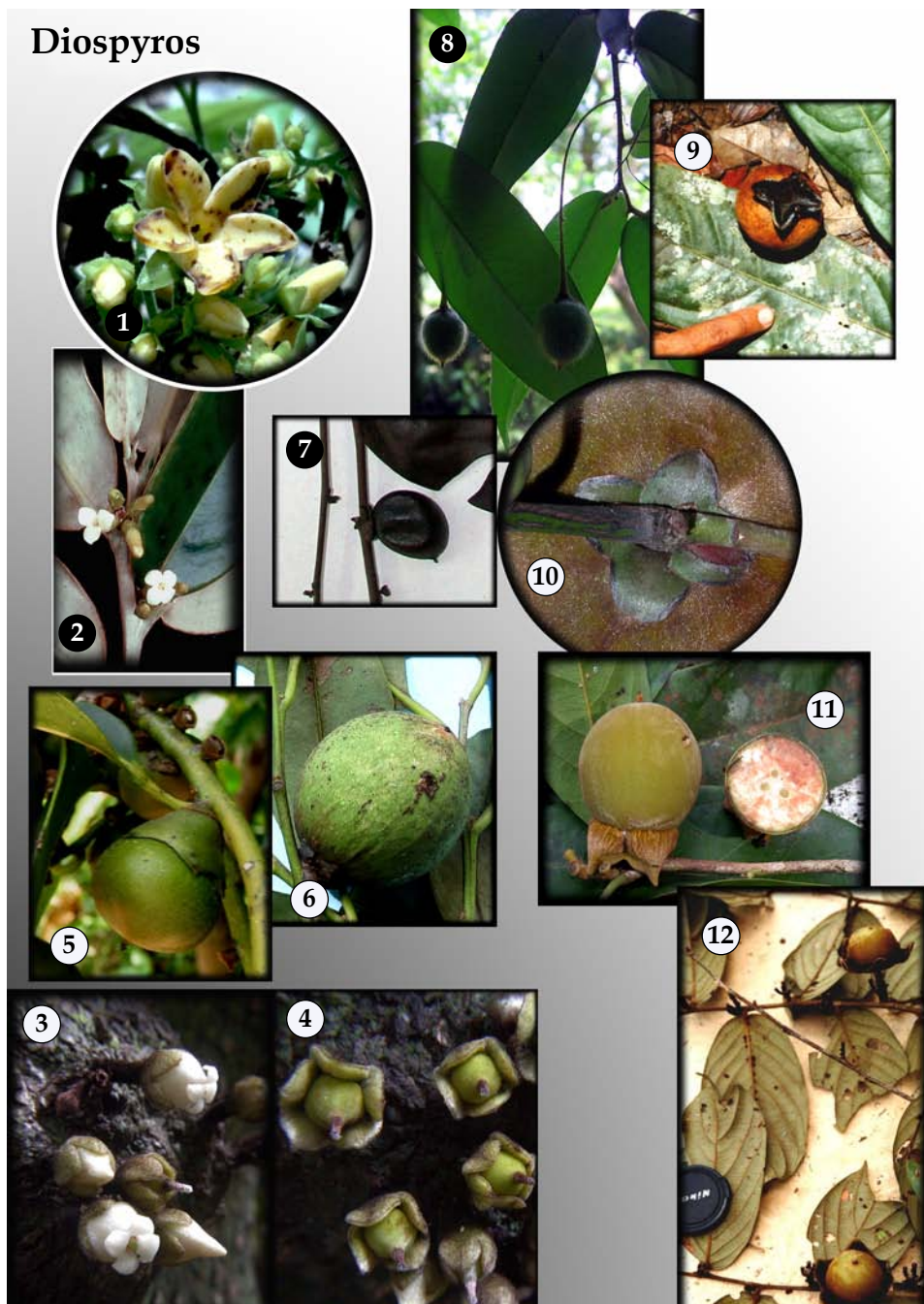
# Diospyros



*Diospyros*, vegetative form. 1, characteristic bark, coal black, thick, often with a greenish cast from surface algae; 2, whatever the outward bark color and form, a cut reveals a thin dark black layer above the pale wood, without exudate; 3, the leaves increase in size from the base of the twig forward, the ultimate leaves smaller again; 4, the branches are arranged like spokes in a wagon-wheel, the leaves of the upright shoot sometimes persistent; 5, the node is simple, a single axillary bud, the pith septate; 6, the node without stipules, the apex is unprotected, pointed, sometimes finely covered with hairs; 7, laminar glands in some species paired near the leaf stalk; 8, laminar glands often appear as yellow or black necrotic dots in the blade; 9, at maturity the leaf glands are often conspicuous and diagnostic to species.



# Diospyros



*Diospyros*, flower and fruit form. 1, *D. latisejala*, the typical corolla is thick and fleshy, white, with a short cup, typically 4-lobed, here with five; 2, *D. argentata*, typical few-flowered inflorescence, here with both three and four petal lobes; 3-4, *D. cauliflora*, here the flower is especially ericoid, the floral bud sharply pointed, the corolla urceolate, the young fruit with four or five calyx lobes; 5-12, calyx and fruit form, critical for species identification; 5, *D. maritima*, the calyx broad but the lobes truncate; 6, *D. toposia*, the calyx highly abbreviated; 7, *D. confertiflora*, diagnostically 3-lobed recurved calyx with curved asymmetric fruit; 8, *D. longiciliata*, atypical long fruit stalk; 9, *D. mindanaensis*, large but typical fruit with 4-part woody expanded calyx; 10, *D. blancoi*, 4-part calyx, overlapping lobes, unusual in the densely feltish fruit surface; 11, *D. wallichii*, with diagnostic thick, warty, recurved calyx lobes; 12, an undescribed species of *Diospyros*, from Lambir, Sarawak, with large fruit and very large inflated 5-part calyx cup. (Photographs 5,6 & 8 © Leonardo L. Co.)

either singly at old leaf axils or in small clusters, rarely in big inflorescences. The corolla is urn-shaped with the petals fused at the base to a varying extent among species, the tips turned back and a slight constriction beneath. The anthers are two-celled, face inward, and split longitudinally. Pistil is one, of two to 12 carpels, locules of the same number, each with two ovules pendent and axial. Characteristic of the genus are the persistent papery or woody calyx lobes that vary in ways that are distinctive of each species. The chromosomes are almost uniformly  $2N=30$  with a few polyploids known.

The vegetative form is sufficiently characteristic that most species of *Diospyros* can be recognized to genus without much effort. (See notes under field recognition.) The tiered branching of the main trunk is unusual in the Ericales, as is the habit of episodic growth in the twigs with leaves of different sizes. The terminal bud frequently aborts. The outer living wood is white and clean while the prized black heartwood is formed in some, but certainly not all species, although only a few species have been surveyed.

The leaves vary greatly in size among species, ranging from thumbnail-sized diamonds of *D. buxifolia* to blades

more than 40 cm long. The blade can be thin and papery or pliable like leather, or as stiff as thick cardboard. The surface varies from shiny and smooth to densely hairy, the hairs are simple, rarely T-shaped.

The calyx usually persists in fruit and is another feature that readily separates many species, varying from small and inconspicuous, to stiff and recurved, to huge inflated envelope. The fruit itself varies from 0.5 cm to more than five cm in diameter, usually green-purple or black-purple, with an outer wall sometimes fleshy but most often hard.

A few species of *Diospyros* are exceptional to most of the rules. *Diospyros venosa*, for example, has a soft white bark and is without whorled branches. There is also variation in germination: foliaceous cotyledons and alternate subsequent leaves versus thick cotyledons and opposite leaves.

The ebonies are characteristic trees of the lowland tropical rain forest, especially within the understory and lower canopy. They are long-lived, frequently flowering and fruiting and show good rates of recruitment and equally high mortality among juveniles. Once established, they grow slowly: few forest grown individuals



*Diospyros*, diversity of bole and leaf form. 1, *D. cauliflora*, the trunk with knobby growths bearing sessile inflorescences; 2, *D. maingayi*, the blade smooth with inconspicuous nerves, drying red and black, the bole widely flared at the base with short rounded buttresses; 3, *D. venosa*, with pale bark, but a scrape shows a blackish inner layer; 4, *D. pendula*, with peculiar smooth finely nerved lower leaf surface; 5, one form of the polymorphic *D. pilosanthera*; 6, *D. buxifolia* with small diamond-shaped leaves, a large columnar bole with tight black bark; 7, *D. latisejala*, large papery leaves that bear stiff silicate hairs, the bark is black and hard, sounding like glass to the scrape of knife; 8, *D. nutans*, a small tree, rarely exceeding 2 cm DBH, with narrow leaves that are weakly invaginated at the base.





*Diospyros blancoi* is an old-fashioned village fruit in the Philippines, called *mambolo* or *mabolo*, the velvet hairs on the outer skin are irritating, the fruit is sometimes seedless, white flesh is very different from the persimmons and tastes similar to *atis*, one of the cultivated species of *Annona* (Annonaceae).

ever grow faster than one or two mm DBH per year. Very few species are weedy, and they do not as a rule favor pioneer communities. The few species that occupy the driest parts of Mainland SE Asia are sometimes fire-resistant and bear a deeply furrowed black bark; a few such species also form branch spines. Rarely we find species that spread by clonal propagation, and this should be looked for in other species. Within the mature forest, individual species are rarely generalists with respect to moisture gradients; rather we find numerous specialists in swamps, some in running water, others on hillsides or ridge tops.

Reproductive ecology is in great need of comparative field study and the genus is so variable that extrapolation from a few species should be avoided. Certainly the bulk of the species appear to be strictly dioecious, but occasional monoecious trees are known and apomixis is not unknown. The cultivated species of the northern latitudes are pollinated by bees. However, the tropical diversity of floral form is great and the single species included in the pollination study at Lambir, Sarawak (of more than two dozen) was beetle pollinated. More than a few of our species are night-blooming and intensely fragrant. In all we might anticipate a mix of beetle, bee and moth pollination.

In some species the inner pericarp eventually softens and is eaten by mammals, and these include the culti-

vated persimmons. More than a few species bear fruit or seeds that are rich in saponins, and are used as fish poisons. Dispersal is probably effected most often by understory mammals and primates.

The genus bears numerous advantages for a student looking for a study group. Within a single forest the individual species are relatively abundant and easily distinguished by vegetative features. They flower and fruit with relatively great frequency and make excellent specimens. Further herbarium study will not likely add much to a knowledge of the ebonies; what the genus needs now is a young student willing to walk the forests and learn the trees, their habits, variation and ecology.



This *Diospyros* from central Vietnam is typical of the species of very dry and fire-prone sites, with a thick black bark and deep sinuous fissures. The small leaves are in short spiral clusters.

## #

### OTHER ASTERIDS: ERICALES

#### MAESACEAE

NAME: From the genus *Maesa*, as below.

OVERVIEW: The family comprises a single genus, *Maesa*, found throughout the Paleotropics, formerly included in Myrsinaceae<sup>1</sup>.

The four families of the Primuloids are a strongly supported clade, as is the sister position of *Maesa*. All share the synapomorphy of free central placentation - in Ebenaceae the ovules are apical-axile and in Sapotaceae axile or basal-axile. Bear in mind that APG III recommends a broad Primulaceae (including what are now four families, Pimulceae, Myrsinaceae, Maesaceae, Theo-

<sup>1</sup> Anderberg, A. *et al.* 2000. *Taxon*. 49: 183-187.

<sup>2</sup> Utteridge, T. *et al.* 2004. *Botanical Journal of the Linnean Society*. 145: 17-43.



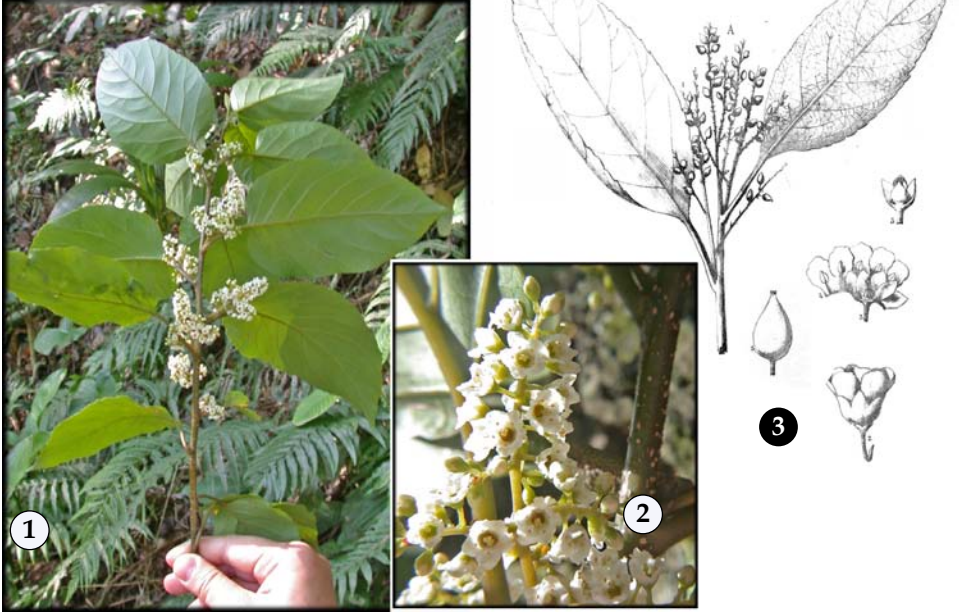
phrastaceae) and that the Myrsinaceae would then be treated as the subfamily Myrsinoideae.

**MAESA.** [From an Arabic name.] A genus of about 100 species, generally the Old World tropics, Africa, India, north to Japan, east to the Pacific and Australia, and including maybe 20-30 or so species in tropical Asia. There is no regional revision but a recent analysis for the Philippines counted 13 species<sup>2</sup>.

*Maesa* species are small shrubs, trees and scrambling lianas, often along water and in full sun. They form a

singular genus, formerly included within Myrsinaceae, but now segregated as its own family. *Maesa* shares with *Ardisia* fleshy leaves lacking stipules and any lignification of the nerves and veins, usually with toothed margins. When dry, the leaves often display a loose pattern of black canals. The flowers are like Myrsinaceae but quite small and arranged in a loose open branched and bracteolate inflorescence. *Maesa indica* is exceedingly widespread, polymorphic, sometimes cultivated.

## Maesa



*Maesa*. 1-3, *M. indica*, arching stream side shrub, here in the Philippines; 1, habit and densely flowered inflorescence; 2, flower; 3, line drawing of plant, habit, flower and fruit. (Drawing from VIDAL *loc. cit.*)

## #

### OTHER ASTERIDS: ERICALES

## MYRSINACEAE

**NAME:** From the genus *Myrsine*, as below.

**OVERVIEW:** The Myrsinaceae are a fairly uniform family but one rich in narrowly distributed, the total currently estimated at more than 1400. These are divided perhaps too finely among 41 genera<sup>1</sup>, although that is a reasonable reduction from more than 120 genera published for the family. In most of the forests of tropical

Asia the family is represented by a single broadly circumscribed genus of understory trees, *Ardisia*. A group of three other genera are found to the east, in the Philippines, Sulawesi and New Guinea, chiefly in the mountains. To those we can add *Myrsine* which occupies the seaside and exposed mountain tops and extends westward to Malaya and sparsely in Mainland SE Asia. Liana *Embelia*, a few herbs, and finally, *Aegiceras* are common small mangroves. The family total for trees of tropical Asia is five genera and about 200 species.

As with the Maesaceae, we can note again that APG III recommends a broad Pimulaceae and that the Myrsinaceae should be treated as the subfamily Myrsinoideae.

In floral form the family is characterized by a single whorl of fused stamens, each stamen borne opposite a

<sup>1</sup>Stähl, B. *et al.* 2004. Families and Genera of Vascular Plants. 6: 266–281.

<sup>2</sup>Pascarella, J. 1997. Brittonia. 49: 45-53.

corolla lobe, and by single loculed ovary with free-central placentation. The five-parted typically bisexual flowers look a bit like the common tomato flower, but the petals are pink, thick and waxy, the fruit a few-seeded berry, drupe or capsule. In vegetative form, the genera share features with various members of the Ericales.

Reproductive ecology has been poorly studied especially in Asia, and so is perhaps too easily generalized as involving bisexual flowers outcrossing via small bees. Some American species of *Ardisia* showed capacity for selfing<sup>2</sup>, while herbarium specimens indicate that more than a few species are unisexual-dioecious. Tropical species bear fleshy berries, mostly red, but a few are blue and black, all greedily taken by birds of the forest understory. Among our species, only the odd mangrove *Aegiceras* has a dehiscent fruit. One of the principle evolutionary plays in the family concerns the length of the inflorescence peduncle, variously positioned from axillary to terminal, pendent or upright, with or without a long basal stalk.

The family has an almost trivial economic value. Only a few *Ardisia* are cultivated, most notably the small potted plant *Ardisia crispa*. Most of our species have the advantage of bearing colorful flowers and attractive red fruits; much more could be done to cultivate these in our native plant gardens. The juice from the stem of *Ardisia fuliginosa* is found Javanese medicine markets, and a few herbs in the family are well-known traditional medicines (e.g., *Labisia*, the Malay *buah Fatimah*), but the trees generally less so. *Ardisia squamulosa* flowers and fruits show up in the Philippine markets.

**ARDISIA.** [Greek, point, supposedly in reference to the pointed corolla lobes, but more likely the pointed stamens.] Worldwide perhaps 250 species, maybe 150 or more in tropical Asia (including *Antistrophe*, *Tetrardisia*). Malaya claims 75 species, the Philippines claims 56 species, about 100 in Borneo. CORNER *loc. cit.* records several Malay names invoking *mata*, or eyes, as in *mata pelandok* in reference to the fruit. The best known name in Borneo is *merjemah*. These are especially diverse in the Asian lowland tropics, but are also abundant in American tropical forests, rare in Australia, and absent from Africa.

These are weakly lignified shrubs, and more than a few of the species in Asia are nearly herbaceous, not reaching even one m in height.

These small trees and shrubs are among the most numerous plants in any particular lowland forest. However, naming them has always been a problem. The main reason is that the vast majority of species, regardless of their local abundance and seeming success, are exceedingly narrow in distribution. Many species are still known from only a single location. This ecological habit - and also the consequent taxonomic problems that follow - are shared with many of the small trees and shrub genera of the Rubiaceae such as *Lasianthus*.

Many species flower and fruit regularly and abundantly and so the berries may form an important food source for understory birds. In this regard, *Ardisia* should be included in the early stages of reforestation. Its main

drawback is that most species are shade-demanding and so can only be planted after an initial canopy develops.

**DISCOCALYX.** [Greek, disc-like calyx.] About 50-80 species, including *Tapeinosperma*, especially in the Philippines, New Guinea, some in Borneo (but not Malaya, nor Sumatra) and then east to the Pacific. These are usually small trees that bear a single somewhat thick main stem with a distinctive terminal bud, hard and pointed with overlapping scale leaves. The blade is variously broad or narrow, often in a strong upright helix, but commonly with toothed margins and otherwise recognizable to family. The genus is poorly represented in the Sunda Shelf. It includes the unusual *D. dissectus* of New Guinea with highly dissected leaves. Several of these species would make excellent native cultivated species.

**LOHERIA.** [Commemorates Philippine collector A. Loher.] A small genus of a few species, especially in the mountains of Philippines, perhaps farther east. So far as is known, the species differ from most *Discocalyx* in the thicker leaves and the long filament of the stamens, but it may well fall nested within the larger genus.

**MYRSINE.** [A Linnaean derivation of the classical name for the myrtle.] This genus is probably best treated broadly as including *Rapanea*, which would make it pantropical and subtropical with at least 150 species or possibly twice that number. These multi-branched shrubs are found high in tropical mountains. In our area *Myrsine porteriana* is very widespread from coastal sand and kerangas to mountains; otherwise, one other in Malaya, Philippines, 10 on Kinabalu several of which are yet unnamed,

#### FIELD RECOGNITION: *ARDISIA*

Small trees and shrubs, weakly lignified twigs and leaves, without exudate.

The point at which the horizontal twigs joins the main vertical trunk is greatly flattened and extended.

The twig apex is often crusted in a deep red pubescence.

The nerves and veins in the leaf blade are dark green against the light green blade, raised faintly if at all, and poorly lignified.

The twigs and leaf stalks are often mottled green and white.

Many species bear bright pelucid glands in the blade, and especially along the margin which can be scalloped or toothed; the glands may not be visible if the blade is very thick.

Often in flower or fruit, and then easily recognized from the immature berries that are typically spotted red and white.

#### FIELD CONFUSION

Other trees with pelucid dots in the leaves include Rutaceae, which are often opposite and/or compound and/or strong smelling, and *Gonystylus*, which is a very well lignified timber tree.

Similar to some saplings of Myristicaceae, but those usually have wagon-wheel branching, and the nervation in *Ardisia* is irregular and includes numerous intermediate nerves.

# **Ardisia**



*Ardisia*. 1, *A. pyramidalis*, in the Philippines, a medium multi-branched shrub with spirally arranged leaves and terminal panicles; 2-3, two other types of floral architecture, 2, a common type with terminal pendent inflorescence of flowers borne in cycles from a persistent main axis; 3, an open lax and pendent inflorescence; 4, the characteristic base of lateral branches, flattened and swollen apically and basally; 5, the twig apex, mottled green and white with finely red hairy slender point; 6-7, the leaf margin is often glandular and sometimes invaginated; 8-9, the flowers typically pink, with a single exerted style and a cone of stamens, are readily recognized; 10, the mature fruit vary from dull green and red to brilliant red. (Photographs 8, 10 © Leonardo L. Co.)





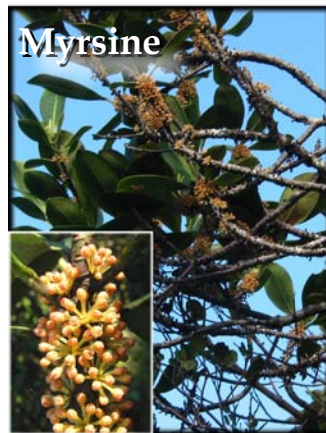
*Discocalyx*. 1, habit, small single stemmed upright tree with a cluster of spirally arranged leaves, a long peduncled inflorescence, axillary from among or below the leaves; 2, the end of the infructescence, flowers produced from lateral branches axillary to densely congested nodes, leafless or with scale leaves; 3, habit showing the spiral arrangement, here *D. linearifolia* with a long and narrow blade. (1 & 2 © Ulysses Ferrar; 3 © Leonardo L. Co)

**AEGICERAS.** [From a Sinhalese name.] The two species of *Aegericus* represent some of our most ubiquitous small mangroves, found everywhere from India to Australia. The Malay is *skang-mata*, or for *A. corniculatum* sometimes a reference to the curved fruit as in the Filipino *saging-saging*. The genus is distinctive among

Asian representatives of the family in that the fruit is elongate and dehiscent rather than the fleshy berry that is otherwise typical, and also in the elongated seed without endosperm. The bark of *Aegiceras* is used as fish poisons. TOMLINSON *loc. cit.* suggests that the two species differ in floral odor and pollinators.



*Loheria*. These are small multi-branched shrubs of the mountains of eastern tropical Asia, basically similar to *Discocalyx*; here, *L. crassifolia*. (© Leonardo L. Co.)



*Myrsine*. Another genus of multi-branched shrubs with spiral leaves, here with floral clusters typically along the leafless stems. (© Leonardo L. Co.)

## Aegiceras



*Aegiceras*. 1-3 *A. floridum* with short uncurved fruit, in Palawan Island, Philippines; 4, *A. corniculatum*, La Union, Philippines, with long curved fruit. These are abundant and common mangroves; typical of the family in the spirally arranged gland-dotted leaves, the flower buds and exerted style pointed and red-spotted; the fruit odd for the family in Asia in the elongate form and dehiscent habit.

## #

### OTHER ASTERIDS: ERICALES

## PENTAPHYLLACACEAE

NAME: From the genus *Pentaphyllax*, as below.

OVERVIEW: The circumscription and nomenclature follows the recommendations in STEVENS (*loc. cit.*) following recent phylogenetic studies<sup>1,2</sup> that segregated *Ternstroemia*, *Adinandra* and *Eurya* from the Theaceae while supporting their association with *Pentaphyllax*. This group of species has also been recognized in some regional literature, with *Pentaphyllax* excluded, and then treated as the family Ternstroemiaceae. Segregation is contrary to the findings of Luna and Ochoterena<sup>3</sup> in a study of floral morphology that was perhaps constrained by limited sampling among Ericales in general, as well as difficulty in establishing homologies and appropriate character states. An interesting study of ITS sequences that focused on species of *Eurya* in Taiwan hinted at significant findings (*Cleyera* nested within *Adinandra*) but the choice of *Ternstroemia* and *Anneslea* as outgroups limits the interpretation<sup>4</sup>. While the Papausian species have been reviewed<sup>5</sup>, there remains much to be done in

the basic taxonomy of the species in the rest of tropical Asia.

PENTAPHYLLAX. [Greek, five-parted in reference to the flower.] Monotypic, *Pentaphyllax euryoides*, from S China, Hong Kong, Hainan and scattered southwards in higher hills and mountains of northern Vietnam, and then distantly to N Sumatra and the Main Range of Malaya. Whether this is the result of long-distance dispersal or a relictual distribution is not known.

This is a small tree with spirally arranged leaves that lack a decisive or clear stipule (although the account in the *Flora of China* describes a “persistent stipule”); the stalk is short, the blade is glossy, the margin is without teeth or glands, and dries yellow. In flower, it gives the appearance of a *Symplocos* or *Theaceae* with short axillary racemes of small white open flowers. The flowers bear two persistent bracteoles close to the five-parted calyx (overlapping, unequal lobes), five petals (basally fused?) and five stamens, inflexed in bud, shorter than and alternate with the petals. The dehiscence of the small two-celled anthers is described as either by valves or apical pores. The five-loculed ovary bears two ovules per locule; the style is long and the stigma is five-lobed. The fruit a capsule, each of five locules opens so as to display the ten seeds. [A photograph appears in THROWER *loc. cit.*].

ANNESLEA. [Commemorates George Annesley, d. 1844, English naturalist.] A genus of about three species from Myanmar to Taiwan, south to Sumatra. The most

<sup>1</sup>Prince, L. *et al.* 2001. American Journal of Botany. 88: 2309-2320.

<sup>2</sup>Wu, C. *et al.* 2007. Botanical Studies. 48: 97-116.

<sup>3</sup>Luna, I. *et al.* 2004. Cladistics. 20: 223 - 270.

<sup>4</sup>Barker, W. 1980. Brunonia. 3: 1-60.



common is *Anneslea fragrans* with a geographic distribution similar to that of *Pentaphylax*. The trees are likewise similar in the form of leaves and flower, the only significant difference is that the flowers of *Anneslea* bear more numerous stamens in one or two whorls.

**ADINANDRA.** [Greek, crowded stamens.] Be careful in spelling because *Adenandra* with an 'e' is a genus of African Rutaceae. The best known species of *Adinandra* is *A. dumosa*, called in Malay *tetiup* or *tiup-tiup*. It is one of the most abundant small trees in nutrient poor, acidic and degraded lands, sometimes forming monodominant patches. Otherwise, the genus includes another 70 species, most poorly known, 15 on Kinabalu, eight in the Philippines. These trees differ from *Cleyera* in that *Adinandra* bears flowers with three-five celled ovary, each cell with up to 100 ovules which mature as seeds less than one mm long, whereas in *Cleyera* we find fewer locules, fewer ovules and larger seeds. An abundant tree of mountain forests in Malaya is *A. villosa*, distinguished by the densely velvety lower leaf surface, sometimes as *jalong* in Malay.

**TERNSTROEMIA.** [Commemorates Swedish naturalist of China, C. Tärnström, d. 1748.] *Ternstroemia* is a pantropical and subtropical genus that differs from other genera in the family in the large flowers (up to two-five cm across) and in the ovary which bears one or few ovules that mature as large seeds, up to one cm across, each with a fleshy red outer layer. Among dried specimens, *Ternstroemia* is recognized by the typically rough pimpled surface of the blade, sometimes almost sandpaper-like, with a red or black color indicating aluminum accumulation.

*Ternstroemia* comprises no more than 80 species, a few cultivated shrubs are well-known, but most of the



*Anneslea fragrans*, adapted from Plate 5 in Wallich's *Plantae Asiatica Rara* of 1829.

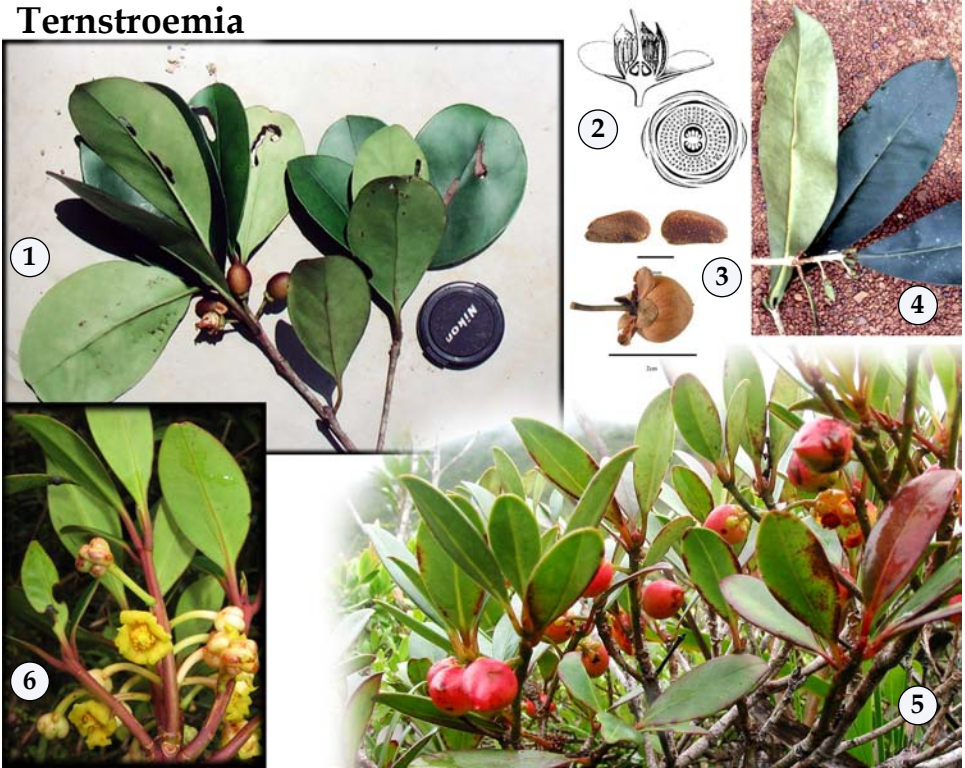
the species of tropical Asia are uncommon. The Malay Peninsula claims eight species, divided between the lowlands, especially swamps, and mountains. *Ternstroemia cornerii* is among the better known members of the genus in Malaya. In Pasoh, it was a slow growing shade-loving tree of the lower canopy, restricted to the wettest



*Adinandra*. Left, a small tree from Lambir, Sarawak, related to *A. villosa*; right, *A. dumosa*, with young fruit, Lambir, Sarawak, the leaves 7 cm long.



# Ternstroemia



*Ternstroemia*. 1, a distinctive species of *Ternstroemia* from Lambir, Sarawak, it dries with a bright red color and strong sandpaper texture, but it remains unnamed; 2, drawing of dissected flower and floral diagram, *T. brevipes*; 3, dried fruit and seed of *T. tepezapote*; 4, *T. cornerii*, Pasoh, Malaya, showing the fresh leaves and young fruit from twig; 5, an unnamed species of *Ternstroemia* from Mt Hamiguitan, Philippines; 6, an unidentified species of *Ternstroemia* from Mangan, Philippines, with large yellow flowers; (Drawing 2 adapted from BAILLON *loc. cit.*; photograph 3, public domain image from ARS-GRIN; photograph 5 © Leonardo L. Co; photograph 6 © Ulysses Ferreras.)

ground, and yet with a low mortality during dry years of the late 1990s when so many swamp species perished. Five species were found at Lambir, all scattered at low density across the plot, and none over 25 cm DBH. Nine species are found on Kinabalu, understandably not well-named. Five species extend east to New Guinea and *T. cherryi* reaches north-eastern Queensland.

In two species of *Ternstroemia* in Amazonia, the flowers were buzz pollinated by bees, but they lacked the poricidal anthers we would normally expect for buzz-pollinated flowers, and instead the dehiscent anthers were closely bound in a floral tube, the small opening of which served as the pollen exit<sup>5</sup>. Nothing much is known about the pollination of Asian species.

The economic potential of the genus is unexplored. *Ternstroemia gymnanthera*, an abundant shade tolerant understory tree of China and Japan, is widely cultivated as an ornamental because the new leaves flush a pretty red. It is now naturalized in Florida.

EURYA. [Greek, in reference to the broad petals.] A genus of the cold northern parts of Asia with many species difficult to segregate. *Index Kewensis* lists over 300 basionyms. MABBERLEY *loc. cit.* generously suggests 70 species, but *Flora of China* claims 130, with 83 in China of which 63 are endemic. Malaya has three, especially *E. acuminata*, found in full sun everywhere from lowlands to mountains. Four species are recorded for Kinabalu, and eight in the Philippines. These are small trees, evidently always with unisexual flowers, the plants dioecious. The leaves are two-ranked, the blade margin usually finely toothed, and in this they differ from the other members of the family and offer an appearance closer to Theaceae. Flowers are congested in the leaf axils or on leafless branches, each flower about seven mm across, stamens number five to 35 in one whorl. The ovary bears two-five cells with three to 60 ovules per cell, placentation axile. Fruits are berries with two to 60 black, shiny, pitted seeds per cell. The common and abundant *Eurya acuminata* is called *legai* in Malay. It is often found growing with small-leaved species of *Symplocos* with which it can be confused. The flowers of

<sup>5</sup>Bittrich, V. *et al.* 1993. *Plant Systematics and Evolution*. 185: 1-6.



*Eurya* aff. *coriacea*, shrub on exposed outcrop, from Mingan, Philippines (© Leonardo L. Co.)



*Cleyera japonica*, from Mingan, Philippines. (© Ulysses Ferreras.)

*Eurya* are often described as malodorous, and this is true at least of the cultivated *E. japonica*.

**CLEYERA.** [Commemorates A. Cleyer, d. 1698, German doctor, mercenary, plant collector in Java and Japan.] A genus of about 24 species in east Asia, tropical America, nine in China, a few reach northern Vietnam, and *Cleyera japonica* south to the Philippines. *Cleyera*

flowers bear two-three locules with fewer than 16 ovules per locule, seeds one-two mm. *Cleyera japonica* is widely cultivated in the warmer parts of the North Temperate Zone including Japan, China and the southern United States. The Japanese name *sakaki* is widely known; twigs of the shrub are important in Shinto rituals in Japan. Note that the common name 'Japanese Cleyera' is often, but wrongly, used for the cultivated *Ternstroemia gymnanthera*.

## #

### OTHER ASTERIDS: ERICALES

## THEACEAE

**NAME:** The family name follows from the old genus *Thea* once used for the tea plant, now as *Camellia sinensis*, even though that name is no longer used. Many individual species are well known in local languages.

**OVERVIEW:** A family of seven genera and 195 species, especially numerous in Temperate and tropical Asia and also in eastern North America. With the genera of the

Pentaphylacaceae removed, the Theaceae are strongly monophyletic<sup>1,2</sup>. Close to *Saurauia*, but that genus lacks the small bracts below the calyx ('prophylls') that characterize Theaceae. The flowers can be superficially like that of some Myrsinaceae. The genus *Ploiarium* was formerly placed here, but is now in the Bonnetiaceae owing to its contorted rather than imbricate petals, while molecular evidence strongly supports the families placement within the Clusiaceae alliance.

The Theaceae are woody plants, small to medium trees and multi-branched shrubs. The calyx and corolla are spirally arranged, sometimes similar to one another. The fruit is a dry capsule with flat seeds. Single, large and axillary flowers are characteristic and so distinguished the family from the otherwise similar Symplocaceae which bear small flowers in axillary clusters. Several additional genera might be noted from the

<sup>1</sup>Yang, S. *et al.* 2004. *Plant Systematics and Evolution*. 248: 45-55.

<sup>2</sup>Prince, L. *et al.* 2001. *American Journal of Botany*. 88: 2309-2320.

<sup>3</sup>Tianlu Min *et al.* 2007. *Flora of China*. 12: 366-478.

# Camellia



*Camellia sinensis*, the tea plant, from BAILLON *loc cit*.

Himalayas and China southward to the northernmost mountains of Mainland SE Asia. For example, we might also have included *Stewartia laotica*. For these you might consult the family treatment for the Flora of China<sup>3</sup>.

**CAMELLIA.** [Commemorates, George Kamel, a Moravian Jesuit missionary in the Philippines, d. 1706.] The species number between 100 and 150 and are distributed from Japan to the equator. Other than the cul-

tivated tea, *Camellia sinensis*, these are rare mountain shrubs in our region, most common in the north of Mainland SE Asia. We have no record for Malaya, one species on Kinabalu, and five in the Philippines including the not uncommon *C. lanceolata*. Photographs of flowers of four Chinese species appear in THROWER *loc. cit*.

**POLYSPORA.** [Greek, many seeded.] *Polyspora* is represented by nine species in Malaya, six in Sabah, with one in New Guinea, two in Thailand, another in Vietnam and Laos. Most of these are poorly studied. The genus *Gordonia* was based on the American loblolly-bay, *G. lasianthus*, and over the last century the genus was expanded in concept to include the Asian tropical trees of *Polyspora* and the American tropical *Laplacea*. Molecular studies recently confirmed that this inclusion was in error and the Asian trees are more closely allied with *Camellia*<sup>2</sup>. Most of our trees have valid names in *Polyspora*, although they still may appear in some regional literature under *Gordonia*, and at least the common Malayan species, *Gordonia singaporeana* has yet to be transferred.

**PYRENARIA.** [Greek, from pyrene, reference to the stoney seed.] A genus of about 20 species, found in Asia from Japan and N China to the equator, with five in Malaya, four in Sabah, and only one in the Philippines and no further north than Mindanao. These small trees are distinguished by the relatively large fruit, more than three cm across, which is often fleshy and indehiscent. (If the fruit is dry and dehiscent it differs from *Camellia* in that it breaks apart upward from the base.) They are odd for the family in that they seem to prevail in



*Polyspora*. Here illustrated by a species known as *Gordonia singaporeana*, the combination under *Polyspora* has not yet been published; from Bukit Timah, Singapore; a fairly common tree of lowland secondary forests in Malaya, distinguished by the leaf margin, venation; when in flower, obvious in the fallen white corolla and attached stamens that litter the ground around the tree.



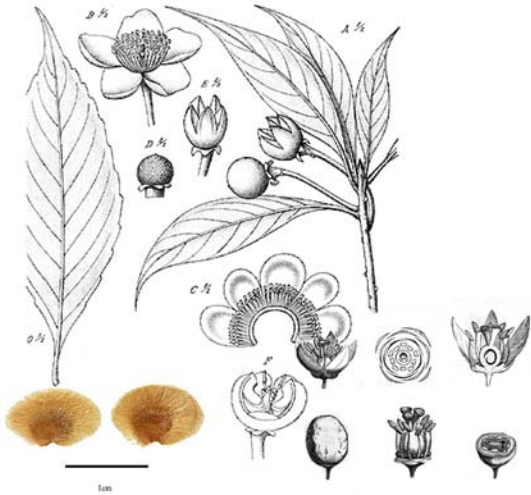


*Pyrenaria*. 1-3, an unidentified species from 1200 m, northern Luzon, Philippines; 4, *P. acuminata*, Pasoh, Malaya, twig apex; 5, *P. acuminata* from southern Thailand, with fleshy fruit and hard seeds.

the lowland forests rather than at higher elevations. *Pyrenaria acuminata* in particular is a widespread and not uncommon small tree, although nowhere abundant. Nothing much is known of their ecology.

SCHIMA. [Uncertain origin.] Sometimes treated as a single polymorphic species, *Schima wallichiana*, but molecular data indicates wide divergence among the isolated mountain forms; up to 20 species may be included. *Schima* becomes abundant in some dry seasonal mountains, the vegetation then called *Schima*-forests.

Schima



*Schima wallichiana*. Drawings from *Atlas der Baumarten von Java* and BAILLON *loc. cit.*; photograph of seeds from USDA ARS-GRIN.

## SYMPLOCACEAE

NAME: From the genus *Symplocos*, as below.

OVERVIEW: Formerly, all 250-300 species were in the genus *Symplocos*. The family is characterized by leaves without stipules, a flower of basic Ericalean organization, that is, at least weakly sympetalous, actinomorphic with epipetalous, numerous, and more or less united stamens, the two-five locules weakly joined usually without a central axis and more or less pendulous ovules, a simple style, and a drupaceous fruit with a hard endocarp. These small trees differ from other Ericales in the inferior or half-inferior ovary and from Theaceae in the smaller flowers, the weak fusing of the corolla and the small racemose axillary inflorescence. Recent molecular work<sup>1</sup> demonstrates the monophyly of the family, and recommends that a few of the most divergent species be segregated as the former genus *Cordyloblaste*.

## CORDYLOBLASTE. [Greek, club-shaped ovary.]

A group of six species of eastern tropical Asia with filaments remarkably fused throughout their length. The ovary is two-locular, the corolla lobes are adaxially papillate, (vs. smooth), the ovary semi-inferior (vs. completely inferior), and the flowers lack the articulation between the hypanthium and the pedicel that characterizes most *Symplocos*. Apparently, these six species are further distinguished by chromosome numbers of 90 rather than the 11 chromosomes typical of *Symplocos*.

SYMPLOCOS. [Greek, woven, in reference to the fused staminal base.] About 250 species widely in the tropics and subtropics of the Americas and Asia with about 80 species altogether in our region. More than a few species are rare mountain-top endemics, more than few yet undescribed. Current tallies include 22 species in Malaya, 18 in Thailand and over 100 in New Caledonia. Malay names include *menasi*, or *nasi-nasi*, and *jirak* commonly in Sarawak.

These are small and medium-sized trees. The vegetative features are described in the Field Recognition. The inflorescence is often branched and open, sometimes congested and sessile with many small white flowers. Other floral features include the inferior ovary with the calyx fused to the outer layer and bearing three-five calyx lobes persistent in fruit. The fruit are typically blue. The petals are shortly fused at the base, the stamens are numerous and fused in a short tube adnate to the



*Cordyloblaste pendula*, Palai, Philippines; the flower with a well developed staminal tube. (© Leonardo L. Co.)

corolla. In contrast to the Theaceae, the carpels do not form a central axis; the placentation is parietal. If the non-articulated floral stalk is ancestral, the presence of articulation is a synapomorphy for *Symplocos* exclusive of *Cordyloblaste*.

Nooteboom has monographed the genus for Asia<sup>2</sup> and made the results accessible over the web in the form of descriptions, images of herbarium samples, and also through interactive DELTA key. Considering the thoroughness of that monograph, I would think that little

## FIELD RECOGNITION: SYMPLOCOS

Ericalean characters - short unswollen leaf stalk, no exudate, no stipule, no odor, margin uneven or with teeth or marginal glands or both.

The blade dries yellow or green-yellow (look for old fallen or withered leaves) but a few species are red.

The blade is said to taste sweet in some species, although I have never confirmed that.

Mostly small, spreading shrubs, especially the mountain plants.

Racemose inflorescences of flowers 5-10 mm across.

Petals only basally fused, many stamens, the ovary is inferior.

The fruit is a blue drupe with germination pores (apical scars) showing the number of seeds.

## FIELD CONFUSION

In mountain habitats, these are easily mixed with other Ericales, especially Theaceae and *Ardisia* and also with *Ilex*.

In lowlands, some species might at first sight be confused with some, *Diospyros*, but are quickly segregated by the toothed margin, and yellow color of dry leaf.

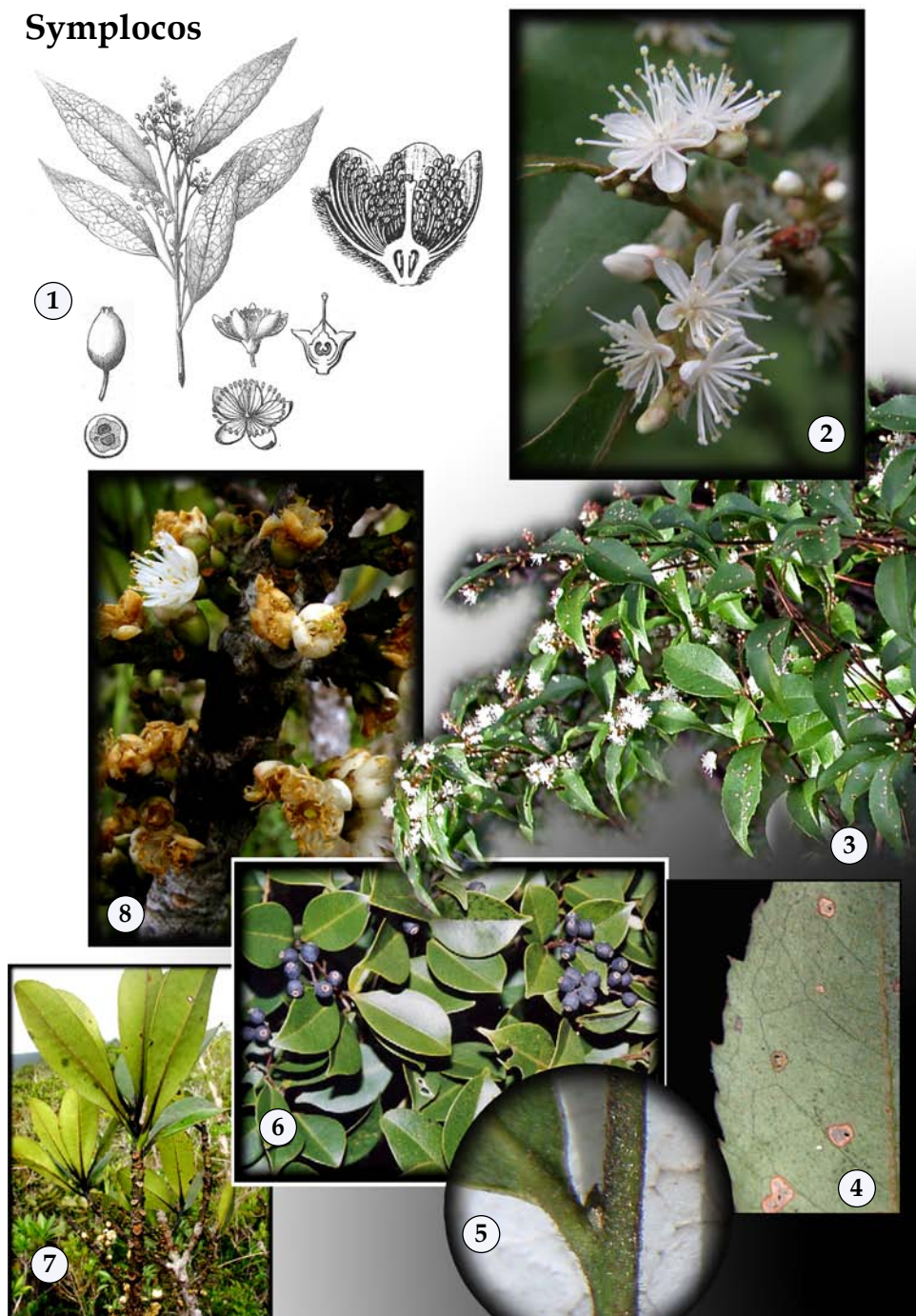
From *Xanthophyllum* because the latter is never with toothed margin and bears distinctive axillary buds, green twigs, oily smell, and glands in the blade.

<sup>1</sup>Wang, Y., et al., 2004. American Journal of Botany. 91:1901-1914.

<sup>2</sup>Nooteboom, H. 2005. Symplocaceae of the Old World: Descriptions, Illustrations, Identification, and Information Retrieval. (<http://www.nationaalherbarium.nl/Symplocosweb/Symplocos.htm>.)

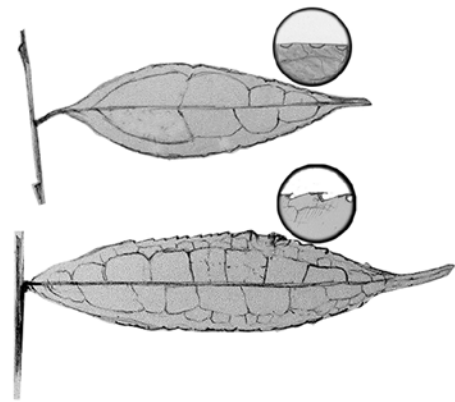
<sup>3</sup>Aranha-Filho, J. et al. 2009 [in press]. Plant Systematics and Evolution.

# Symplocos



*Symplocos*. 1, *S. lancifolia*, habit and details of flower and fruit; 2-5, *S. lancifolia*, Benguet Province, Luzon, Philippines; 2, the flower with spreading stamens nearly free to the base; 3, a showy display of flowers from small branched inflorescences; 4, toothed leaf margin; 5, short unswollen leaf stalk, without stipules, the axillary bud silky hairy; 6, a *Symplocos* from Mt. Hamiguitan, Philippines, yet unidentified to species; 7-8, *S. aff. polyandra* illustrates a type of *Symplocos* found in open exposed mountain tops, with a spiral of leathery leaves and flower nearly sessile below, from Mt. Hamiguitan, Philippines; (Drawing in 1 adapted from Plate 64 of VIDAL *loc. cit.*; photographs 6, 7 &-8 © Leonardo L. Co.)





Comparison of the leaves of common roadside shrubs, *Symplocos adenophylla* (above) and *Eurya acuminata* (below).

purpose is served in any student pursuing a further revisionary analysis of herbarium specimens. What is now needed is extensive field study of pollination, dispersal and physiology. Many South American species display cryptic dioecy, that is, flowers possess stamens and ovaries but the flowers function unisexually. The term functional unisexuality is also applied to Asian species based on the appearance of herbarium specimens. At least some species bloom at night and then remain open for part of the next day, but there is little comparative observation.

The physiological ecology of *Symplocos* is likewise little explored. While they are a conspicuous part of the upland flora, especially abundant in exposed summits, *Symplocos* are also found as a very minor member of the lowland forests, sometimes as obvious gap colonists, but more often in the fashion of *Symplocos crassipes*. This



*Symplocos crassipes*, Pasoh, Malaya, a common small shrub with nearly sessile leaf and slightly invaginated base.

common species, of which a good population was found in the Pasoh Forest plot, was not a gap species. Rather, *S. crassipes* appear to be shade-tolerant as a recruit, with many of the scattered small trees persisting for 20 years without significant growth, and yet a few individuals showed rapid growth between 5-15 cm DBH followed by death.

#

OTHER ASTERIDS: ERICALES

CLETHRACEAE

NAME: From the genus *Clethra*, as below.

OVERVIEW: A small family of two genera and 75 species. *Clethra*, as below, and *Purdiaea* comprises 11 species of the American tropics, chiefly in Cuba.

CLETHRA. [Greek name for the alder, in reference to the superficially similar leaves.] Maybe 65 species, distributed in Eastern Asia, tropical uplands, in southeastern North America, to Central America, and one species in Europe.

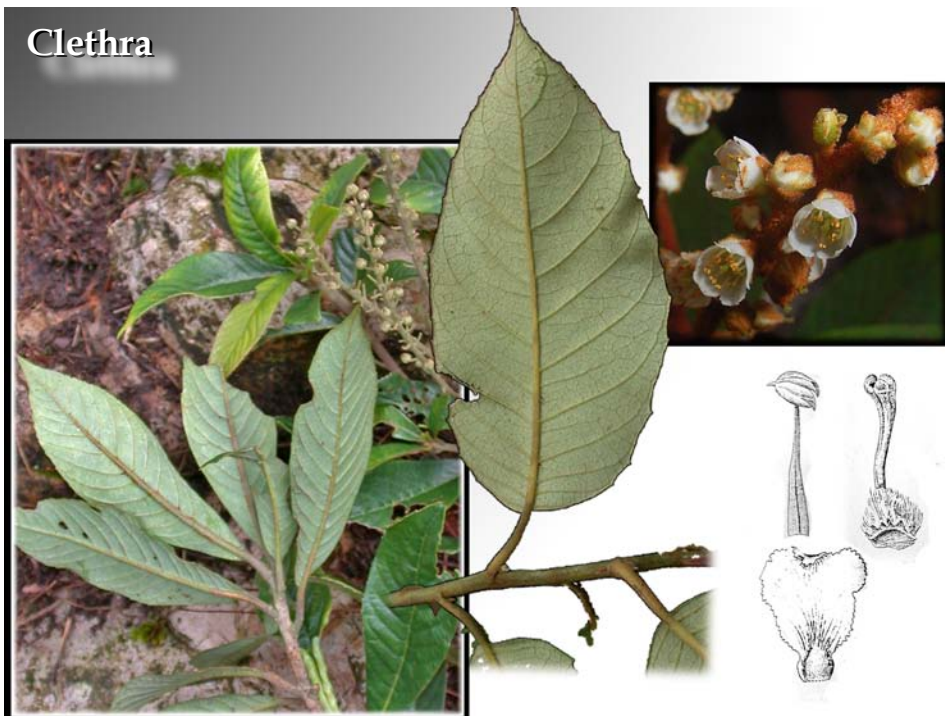
These are small trees or shrubs with leathery evergreen leaves, clustered in a spiral array at the end of

long branches. The leaf stalk is relatively long, the node without stipules. The blade margins are usually toothed while the axils of the pinnate nerves often bear domatia of hair tufts. Stellate hairs are common and most of our species have a white lower surface. The flowers are borne in fairly long spikes, often long persistent. The flowers are small, sometimes fragrant, regular with parts in fives. The corolla is mostly white, the stamens number 10 (rarely two), free of the perianth (or no more than barely fused to the petal bases. The anthers are distinctive in spear-like shape and dehisce by pores. The gynoecium comprises three carpels, the fruit a dehiscent capsule.

*Clethra* species are primarily shrubs of the mountains, found in open places over 1000 m. Occasionally they are found at lower elevations, especially in exposed, degraded or fire prone areas. China counts seven species, three endemic; *Clethra hendersonii* is widely distributed in the upper mountains of Malaya, three in Borneo, four species in the Philippines.

Anderberg, A. *et al.* 2002. Organisms, Diversity and Evolution. 2: 127–137.

# Clethra



*Clethra canescens*, Philippines; left, with young fruit in racemes; center, the leaf and twig; upper right, flowers; drawings of stamens and petal (Photograph of flowers © Leonardo L. Co; drawing adapted from *Icones Bogoriensis*.)

## #

### OTHER ASTERIDS: ERICALES

## STYRACACEAE

NAME: From the genus *Styrax*, as below.

OVERVIEW: A fairly narrowly defined family of about 130 species of *Styrax* and another 40 species in 11 other genera, distributed in warm temperate and tropical parts of America, Europe and Asia. These are all woody plants with spirally arranged leaves, lacking stipules but often with a conspicuous white stellate indumentum. The body is resinous, the leaf blade margins are toothed, the inflorescence basically racemose and without bracteoles. The flowers are bisexual, five-merous with a small calyx and a more or less inferior ovary, the fruit a capsule or drupe. These were formerly associated with *Diospyros*, and the fruits of at least *Styrax* do look similar, but they are now placed variously near Symplocaceae.

In ecology, these are all trees of the strongly dry seasonal forests and only *Styrax benzoin* shows up sparsely in the lowland forests of the Sundaic Region. We could add a few additional genera from the northernmost mountains of Mainland SE Asia. *Rehderodendron* reaches northern Vietnam and *R. kwangtungense* is illustrated in flower in THROWER *loc. cit.* Likewise, *Parastyrax* might yet be documented for Vietnam and Thailand.

STYRAX. [From a classical Greek name for *Styrax officinalis*, probably derived by corruption from Arabic.] Over 300 basioyms, representing about 130 species, monophyletic, worldwide in the tropics and subtropics with nearly a dozen species in Mainland SE Asia. *Styrax* differs from other genera in the family in that the staminal tube attaches high on the petals, the ovules bear two integuments and the seed has a hard thick coat. *Styrax benzoin* is a fairly common tree in much of Mainland SE Asia; it is found more patchily and at lower densities as we move south into the lowland equatorial forests of the Sundaic Region. It is patchily common in some secondary forests of the Malay Peninsula. In Borneo, we find only *S. agrestis*, and only in the southern half of the island, while the genus is absent from the Philippines ex-

Fritsch, P. 1999. Systematic Botany. 24: 356-378.

Fritsch, P. 2001. Molecular Phylogenetics And Evolution. 19: 387-408.

# Styrax



*Styrax*. Left, *S. benzoin*, Pasoh, Malaya, inset of the leaf with whitish lower surface; right, the leaves of *S. agrestis*, Botanic Gardens, Ho Chi Minh City, Vietnam.



*Styrax benzoin*, from Thailand, adapted from BUNYAVE-JCHEWIN *loc cit*.

cept for sparse populations of *S. japonicus* and only in northern Luzon.

*Styrax benzoin* is tapped for benzoin resin, called in Malay *kemenyan*, a name also applied to the tree.

**BRUINSMIA.** A genus of two species, *Bruinsmia polysperma* from Assam to Myanmar, and the more common species, *B. styracoides*, found sparsely in seasonally dry parts of Sumatra, Java, east Borneo, Mindanao to New Guinea.

*Bruinsmia* is distinguished from *Styrax benzoin* by the leaves, which are glabrescent or sparsely stellate hairy, by the compound dichotomous inflorescences (as opposed to racemose-paniculate), the articulate flower-stalks, the free petals, the three- to five-celled ovary and fruit, and by the many seeds in the fruit. (Not illustrated.)

**ALNIPHYLLUM.** [Greek, alder-like leaf.] A small genus of about three species found in SW China, Taiwan, and sparsely in the northern parts of Mainland SE Asia, for example, *Alniphyllum fortunei* in Laos. The fruits of *Alniphyllum* are dehiscent capsules with numerous winged seeds. (Not illustrated.)



ERICACEAE

NAME: From the genus *Erica*, European heaths.

OVERVIEW: A family of small trees and shrubs, diagnosed by the bell-shaped flowers, with stamens twice the number of corolla lobes in two whorls from the base of the corolla tube, and the bulk of the family (the advanced members) further distinguished in that the anthers are inverted at maturity and open by a terminal pore.

A typical species of Ericaceae in tropical Asia is a multi-stemmed shrub found either in high mountains above 1200 m, or on nutrient poor exposed lowlands such as white sands or as epiphytes in mangroves, peat swamps or riversides. The leaves are simple, leathery, entire or finely serrate, most often spirally arranged or sometimes opposite, bearing small urn-shaped flowers 5-10 mm long or large and very showy bell-shaped flowers to seven cm long. These are bisexual, usually in an axillary raceme. The parts are in fives, the calyx papery, the corolla a tube with overlapping lobes that bears anthers in two whorls, twice the number of corolla lobes, usually from the base of the tube. The ovary is superior

or inferior and the fruit a capsule or a fleshy berry with numerous seeds.

The phylogeny of the Ericaceae was one of the earliest beneficiaries of *rbcL* data, and has continued to advance since then<sup>1</sup>. A current account of the family phylogeny is maintained by Professor Kathleen Kron at Wake Forest University<sup>2</sup>.

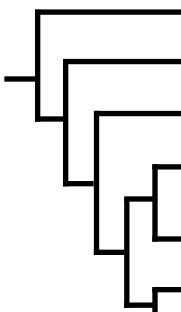
Is the family Ericaceae important in tropical Asia? For much of the 20th Century the family was described as a feature of the North Temperate Zone with minor representation in the tropical mountains, while the Epacridaceae was seen as the Australian equivalent with minor incursion westward. Two things have changed that view. First, the new phylogenetic arrangement illustrated here nests *Styphelia* and allies of the former Epacridaceae within the Ericaceae between the other large clades of the heaths and blueberries. Second, several decades of critical taxonomic work has clarified the species representation in Asia and its distribution. The result is that the family is now seen as evincing an exceedingly complex geologic history with major centers of species richness in Mainland East Asia and North America, in S Africa, in Australia, and also with a center in New Guinea. Most relevant to the region covered in this volume are the two genera *Rhododendron* and *Vaccinium*. To these we add a minor component of endemics in the circum-Pacific genera *Gaultheria* and *Diplycosia*, although these are rarely more than subshrubs and rarely of any abundance.

Flora Malesiana lists 740 species in 12 genera, but most of that diversity lies in New Guinea, to which is added a special pocket of richness on Kinabalu with over 100 species. (See the illustrations in WONG & PHILLIPS *loc. cit.*) By contrast, the Malay Peninsula records

<sup>1</sup>Kron, K., *et al.* 1993. *Annals of the Missouri Botanical Garden*. 80: 735-741.  
<sup>2</sup>Kron, K. 2008. The Ericaceae Website. (<http://www.wfu.edu/~kronka/kakbek/ericaceae.html>).  
<sup>3</sup>Heads, M. 2003. *Telopea*. 10: 311-449.  
<sup>4</sup>Stevens, P. 1981. in *Biogeography and Ecology in New Guinea*.

Phylogeny of Ericaceae

The phylogeny of Ericaceae below follows the analysis by Kathleen Kron<sup>1,2</sup> in recognizing 7 subfamilies. The former family Epacridaceae is now nested within the Ericaceae and is treated as the subfamily Styphelioideae.

	Subfamily	Diversity & Distribution	Trees of Tropical Asia
	Enkianthoideae	1/15, <i>Enkianthus</i> , Japan to Indochina.	1/2, Mainland SE Asia mountains, not east.
	Monotropoideae	8 genera, saprophytic herbs, and ground perennials ( <i>Pyrola</i> ).	0
	Arbutoideae	2 genera, fruit with bony endocarp, N Temperate shrubs.	0
	Ericoideae	19/1790, includes the azaleas and rhododendrons, cosmopolitan, especially N Temperate.	1/40, (and 150 in New Guinea), <i>Rhododendron</i> , common in uplands, sparsely in lowland white sands.
	Cassiopoideae	1/12, Prostrate shrubs of cold-climate.	0
	Styphelioideae	35/420, Chiefly Australian,	2/5, exposed summits and white sands.
	Vaccinioideae	50/1580, <i>Vaccinium</i>	<i>Craibiodendron</i> , Mainland SE Asia, not east. 2/10, <i>Gaultheria</i> and <i>Diplycosia</i> , possibly nested, high mountains, 1/10, <i>Vaccinium</i> in high mountains.



*Rhododendron*. Upper left, *R. subsessile*, Cordillera, northern Luzon; lower left, *R. javanicum* from Mt Hamiguitan; center, lower leaf surface of a sterile *Rhododendron* with the characteristic golden scales of the Vireya group; upper right, an evidently new species from Mt. Mantalingahan, Philippines; lower right, unidentified species from near Dalat, central Vietnam. (All photos except lower left, © Leonardo L. Co.)

only 32 species, and all of Thailand lists only eight genera and 40 species.

The overwhelming majority of species are found at no less than 1000 m elevation, and more abundantly at 1500 m or more. Perhaps five species can be found near sea level in tropical Asia.

While some Nepalese species of *Rhododendron* can exceed 60 cm DBH, it is rare to find a *Rhododendron* in tropical Asia that can reach even so much as 10 cm DBH. That is true of the other genera as well, and the family is unimportant among the larger classes of trees.

All of these points are by way of conveying a more accurate portrait of the family's importance. The Ericaceae of tropical Asia are species-rich, but severely limited with regard to stature and altitudinal distribution, such that for most of our area of interest the family is insignificant. Lowland forest inventories never encounter the family, and even a one-ha inventory of more than 1200 trees, five cm DBH and above, on Fraser's Hill at 1200 m elevation recorded not a single representative. Certainly a forester could spend their life in the lowland equatorial tropics of Asia and never see an Ericaceae other than *Styphelia*.

While a lowland forester might safely ignore the Ericaceae, there is much in the family to excite the atten-

tion of any young botanist with an interest in phylogeny, geography or horticulture. We might mention here the idea that in many Ericaceae the plant represents an elaboration of the inflorescence with the leaves as modified floral bracts. Another curious feature of the geography and ecology lies in the odd link between the highland habitats that are considered typical for the family and their presence at sea level in nutrient poor locations such as white sands, ultramafics and mangroves. (Further aspects of geography and evolution are considered in the essays by Heads<sup>3</sup> and Stevens<sup>4</sup>.) With regard to horticulture, the mountain rhododendrons are among the most beautiful of all Asian flowering shrubs, and yet how rare to find them cultivated in the Hill Stations.

#### ❧ - Enkianthioideae - ❧

**ENKIANTHUS.** [Greek, enlarged flower, one species with colored floral bracts.] A small genus of six species of shrubs found in China and Japan, popular as cultivated trees, at least *Enkianthus quinqueflorus* reaching sparsely south to Vietnam, Hong Kong and Laos. These are distinguished by the cup-shaped flowers, by pollen shed in monads rather than tetrads; the anther opens by slits and is not inverted in bud as is typical of most Eri-

caceae. Many photographs can be found in the horticultural literature. (Not illustrated.)

☞ - Ericoideae - ☞

## RHODODENDRON.

[Greek, red tree, for the flower.] A diverse genus with an estimated 850 species (or over 1000), more or less cosmopolitan, but especially China with perhaps 600 species, and also with a pocket of 155 endemic species in New Guinea. Only three species extend eastward beyond New Guinea, reaching as far as N Queensland, but not at all in Western Australia. West of New Guinea the genus is also conspicuous above 1500 m, but with reduced richness: 18 in Malaya, about 50 in Borneo with 25 on Kinabalu, 13 in Brunei. The Philippines claims 22 species with complex biogeographic history, some linked to New Guinea, some to the Himalayas. The genus is also in the few high places of Mainland SE Asia. In the equatorial lowlands, the genus is rare and found in specialized habitats such as

leached white sand forests. Also, we might mention *Rhododendron javanicum* as an epiphytic shrub of riverside in lowlands.

The most showy of all mountain shrubs, *Rhododendron* attract enthusiasts from around the world. The American Rhododendron Society is a good place to start learning about these plants; the *Vireya* rhododendrons, the most important section in tropical Asia, have their own excellent web site.

☞ - Styphelioideae - ☞

The family formerly known as Epacridaceae are nested within the Ericaceae. It includes about 400 species that most specialists prefer to split among 20-35 genera. These are chiefly small trees and shrubs, abundant and diverse in Australia, New Zealand and adjacent lands, typically with simple leaves, spiral, crowded, sessile, venation perhaps essentially palmate, but the leaves narrow and venation appears nearly parallel and monocot-like. The flowers are not distinguished from the Ericaceae and share the inverted anther that distinguishes all but the most basal of the ericoid taxa. The tradi-

## Styphelia



*Styphelia malayana*, Mt Hamiguitan, Philippines, flower and fruit; this example appears to differ in some details from the species as it occurs in Malaya and Borneo, the lower leaf surface is lacks the dense white waxy covering. (Photographs © Leonardo L. Co.)

tional distinctions of leaves with parallel nerves, sepals mostly free, anthers 1-celled, are considered derived. Only a few species reach westward to tropical Asia where they typically occupy exposed summits at high or low elevations, or near sea level on white leached sands.

**TROCHOCARPA.** [Greek, in reference to the shell-shaped cells of the fruit.] 12 species chiefly in Australia but *Trochocarpa celebica* west to Kinabalu in Borneo, Sulawesi and the Philippines. Small trees with leaves less than one cm long with three parallel nerves. Flowers with a small calyx, corolla tube about three mm long, the fruits to five mm long, tipped with persistent style and bearing 10 stones. (Not illustrated.)

**STYPHELIA.** [Greek, dense, in reference to the flowers.] 14-20 species of Australian area, but only *Styphelia malayana* (formerly *Leucopogon malayana*) in most of our region. The lower leaf is waxy white. In habitats often associated with *Leptospermum* (Myrtaceae). Strongly mycorrhizal.





*Diplycosia*. Left, *D. luzonica* (Palali, Philippines; center, and unidentified species of *Diplycosia* in flower, from Mangan, Philippines; right, an unidentified species of *Diplycosia* in fruit from the Central Highlands of Vietnam. (Photograph on the left, © Leonardo L. Co; photograph in the center, © Ulysses Ferreras.)

☞ - Vaccinioideae - ☞

**A - Lyonieae - a**

Lyonieae sister to a large clade comprising blueberries and wintergreens, corolla sympetalous, usually urceolate to tubular, the lobes small; stamens usually 10, the filaments usually S-shaped, sometimes with paired spurs on the anther-filament junction or upper portion of filament, dehiscing by terminal pores. Ovary usually five locular, superior; fruit a loculicidal capsule.

**CRAIBIODENDRON.** [Commemorates British botanist W. Craib, d. 1933, author of *Florae Siamensis Enumeratio*.] The genus comprises about five species of China, India and the northern mountains of Mainland SE Asia, *Craibiodendron henryi* most notably. (See photographs in GARDNER *loc. cit.*).

**LYONIA.** [Commemorates J. Lyon, d. 1818, American horticulturist.] A fairly well-known genus of about 35 species with an East Asian-East American distribution. It includes a few uncommon mountain shrubs and small trees, such as *L. ovalifolia* which is very widespread in E Asia and reaches as far south as the Cameron Highlands, Malaya. Peculiar among our Ericaceae in the large soft leaves and spikes of pendent white flowers. It occurs in neither Borneo nor Philippines nor further east.



*Vaccinium*, unidentified to species, from Mangan, Philippines; © Ulysses Ferreras.

## A - Wintergreens & Blueberries - a

A species-rich group of upright and prostrate shrubs, found especially in the cold North but also characteristic of high tropical mountains. The genera are difficult. A group around *Gaultheria* and *Diplycosia* bears methyl salicylate and so has a faint wintergreen odor, while the fruit is a superior capsule or indehiscent berry, typically with a fleshy calyx. The blueberries themselves are characterized by an inferior ovary with the small calyx lobes usually persistent at the top of the berry. *Vaccinium*, when traditionally and broadly defined, is polyphyletic. *Agapetes* is interdigitated with *Vaccinium*. *Dimorphanthera* is abundant in New Guinea, not in Borneo, but with two rare species of mossy forests in the Philippines. *Costera*, especially *C. ovalifolia* as an epiphyte in mangrove and peat swamps.

**DIPLYCOSIA.** More than 100 species of tropical Asian mountains, especially Kinabalu

with more than 20, four in Brunei, at least six species in the Philippines, five in Malaya.

**GAULTHERIA.** [Commemorates Galtier, d. 1751, a French-Canadian botanist.] 135 species in tropical mountains except Africa; a few in Mainland SE Asia, two in the Philippines, one on Kinabalu.

**VACCINIUM.** [Classic name for *V. myrtillus* of Europe.] By tradition with 450 species, cosmopolitan, abundant in northern latitudes, but especially in the north, but with 120 New Guinea, 15 in Malaya, 12 in Brunei, 33 species in Philippines and 17 on Kinabalu. Molecular evidence demonstrates the genus is polyphyletic. The Asian species evidently belong to two different clades, one - *Agapetes* clade - is closely related to the temperate Asian species of *Vaccinium*.

## #

### OTHER ASTERIDS: ERICALES

## ACTINIDIACEAE

**NAME:** From the genus of lianas, *Actinidia*, the name from Greek in reference to the radiating styles. It includes the kiwi-fruit, *Actinidia deliciosa*.

**OVERVIEW:** This is a small family of three genera and about 360 species, most of these in the genus *Saurauia*, as below. They are found in temperate and tropical regions of Asia except for about 80 species of *Saurauia* in C and S America. In the past, the Actinidiaceae were allied with *Dillenia*, a relationship that has been falsified by molecular data and the current position as a relatively derived element of the Ericales now seems secure<sup>1,2</sup>.

**SAURAUIA.** [Commemorates Franz Graf van Saurau, 19th century Austrian politician.] Over 500 basionyms represent perhaps much fewer than 300 species, about 80 in the Neotropics and the rest in Asia. We find six species in Vietnam<sup>3</sup>, 10 species claimed for Malaya, 17 for Kinabalu, while 55 species claimed for the Philip-

pines and another 50 in New Guinea, which suggests the propensity to form local races among these small trees of wet mountains. The common Malay name is *mata ikan*, or fish-eyes, in reference to the fruit like globes filled with a slimy jelly.

These are soft wooded trees and shrubs with spiral leaves, no stipules, flowers five-merous, radially symmetric, sepals free, petals fused at the base, stamens many, joined to the corolla, ovary superior, styles free, as many as the ovary cells, ovules numerous and axillary, the fruit a berry. The leaf blade is often rough hairy with a strongly toothed margin, the stalk sometimes disproportionately long and varies in length along a branch. The flowers are bisexual in form yet they may function unisexually in some species.

In ecology, these are almost all arching shrubs found on the banks of streams and broken hillsides. They are particularly prevalent between 1000 and 1500 m elevation. The genus includes many species with attractive flowers; *S. klemmii* is a magnificent cauliflorous tree in Luzon, over 10 cm DBH at maturity, with masses of white flowers from branched inflorescences.

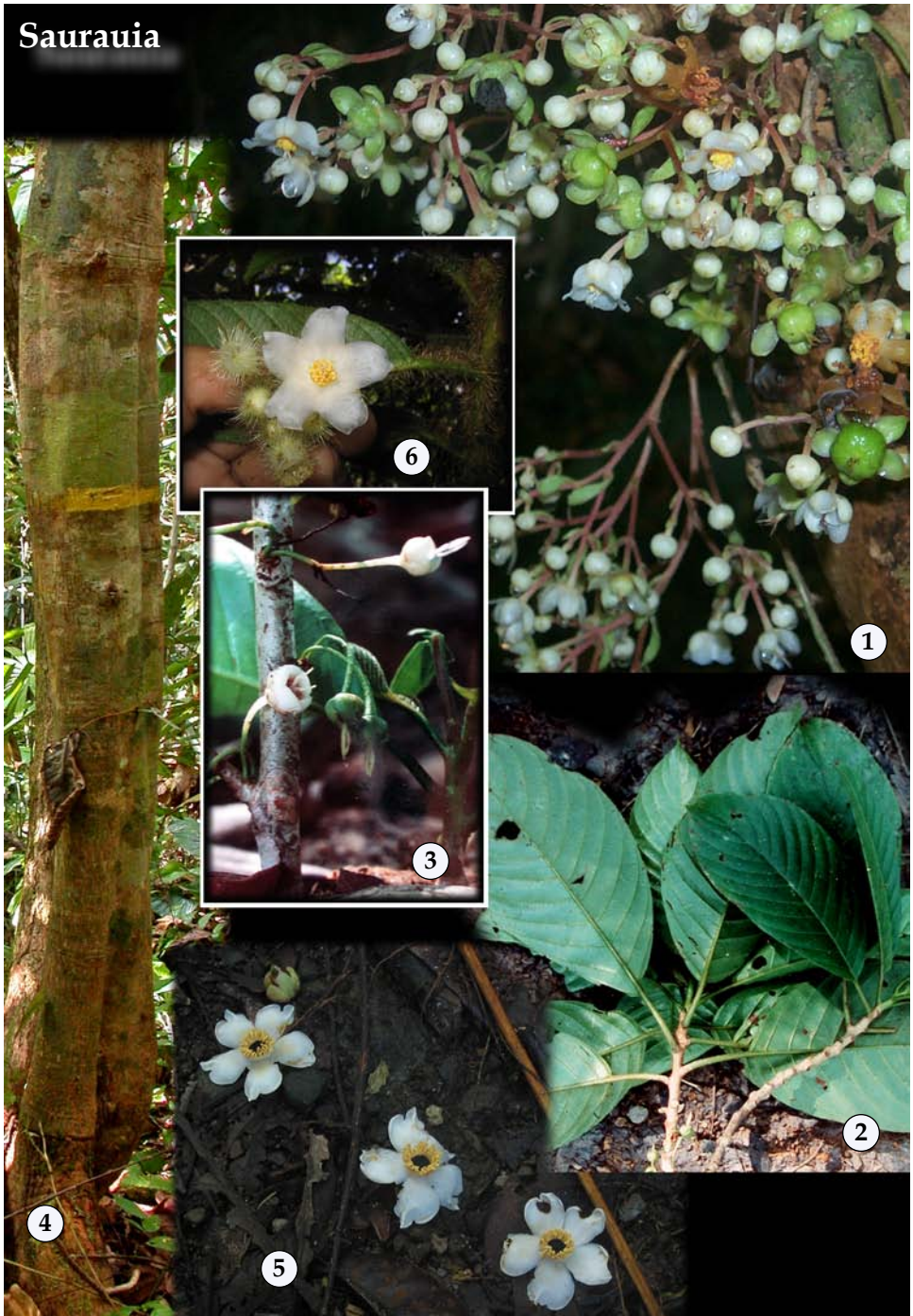
That there is no comprehensive guide to the genus in Asia is a missed opportunity. The genus is easily recognized as are most of the individual species. Of particular interest to students of geography and phylogeny, *Saurauia* is also of potential significance to the horticulturist. As small shrubs and trees, they are readily accessible and make relatively good specimens; and although many species are narrowly distributed, they are typically abundant along the streams and hillsides where they occur.

<sup>1</sup>Anderberg, A. *et al.* 2002. American Journal of Botany 89: 677-687.

<sup>2</sup>Schönenberger, J., *et al.* 2005. International Journal of Plant Sciences. 166: 265-288.

<sup>3</sup>Cuong, N. *et al.* 2007. Blumea. 52: 209-243.

# Saurauia



*Saurauia*. 1, *S. klemmii*, Philippines, a fairly large cauliflorous tree with branched inflorescence; 2-4, an species from Lambir, Sarawak, locally well-known, but not yet formally named; 2, the flowers arranged in a fashion most typical of the genus, singly or in clusters from the twig below the leaves; 3, the flowers with long persistent style, the corolla here not showy, with reflexed tips; 4, a mature tree that measured 4.5 cm DBH in 1993 and 12.8 cm DBH in 2003; 5, *S. latibractea*, Mt. Makiling, Luzon, Philippines, the fallen corollas with numerous stamens attached to the base; 6, *S. trichophora*, Migan, Philippines, densely hairy, the flower with a spreading corolla. (Photographs 1 & 4 © Leonardo L. Co; 5 © Ulysses Ferreras.)